Long-term landscape dynamics in a Caledonian pine forest

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Declaration

I hereby declare that the work in this thesis is my own, except where otherwise stated, and that it has not been previously submitted in application for any other degree.

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Abstract

An understanding of long-term landscape dynamics provides a useful foundation for present and future management planning. Most long-term processes operate outside human timescales, so this thesis uses a combination of palaeoecological records and pollen dispersal modelling on an important threatened ecosystem, the Caledonian pine forest, to i) reconstruct feasible past landscapes using novel methods ii) study the long-term dynamics leading to community transitions within the landscape. The overall aim is to increase understanding of the role of processes such as fire and human activity on landscape dynamics in the second half of the Holocene and the development of the present day mosaic. Firstly, the performance of the Prentice model of pollen dispersal is assessed against modern vegetation and pollen assemblage data at Abernethy Forest, Inverness-shire. The model performed well for the major landscape forming taxa (*Pinus*, *Calluna*, *Betula* and Poaceae/Cyperaceae), but less well for taxa occurring infrequently in the modern vegetation such as *Alnus*, *Salix* and *Corylus*.

Secondly, stratigraphic, pollen, charcoal and tephra data from the analysis of seven peat cores are presented. The data imply that once *Pinus sylvestris* became dominant in the region c. 7000 BP, little change in forest composition, openness and fire regime occurred until c. 4000BP, when human activity began to affect the region. Cyclical heathland-forest transitions become established in some locations from around 3000 BP. Hypotheses are then advanced linking major processes to vegetation dynamics, and used as the basis for simulation of possible past vegetation mosaics at two key time slices, defined by the Hekla-4 (3830 BP) and Glen Garry (2100 BP) tephra isochrones.

Thirdly, the Prentice model of pollen dispersal is applied to these possible mosaics to simulate pollen assemblages at the coring locations, which are statistically compared with the fossil assemblages to identify the most feasible landscape mosaic for each time slice. These landscape mosaics are in themselves valuable contributions to debates on the 'natural' state of the studied area and the effects of different management and environmental regimes. They also permit refinement of the hypotheses connecting process and vegetation dynamics for Abernethy Forest over the long term ($10^2 - 10^3$ years). Finally, suggestions for how these techniques can be best applied to informing conservation management are made, together with discussion of strengths and limitations of the approach and future directions such work could take.

Plant and pollen nomenclature

Vascular plant species nomenclature follows Stace (1997) and pollen taxonomic groups follow Bennett (2005). Where more than one species for a particular genus is under discussion, full scientific names are given; otherwise, after the first reference, only the genus is given.

Age estimates

Unless otherwise stated, all radiocarbon dates cited are rounded to the nearest 50 ^{14}C years for errors of ± 50 years, and to the nearest 100 years for errors ± 100 years. All age estimates are expressed as calibrated calendar years BP (cal. BP) and, in parentheses, ^{14}C radiocarbon years before present (BP). Where frequent reference is made to an age estimate, cal. BP only is cited after the first reference. Calendar ages were calculated using CALIB 5.0.1. (Stuiver et al., 2005) using the IntCal04 calibration curve (Reimer et al., 2004). Present is taken as AD 1950.

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Chapter 1. Reconstructing landscape dynamics in Caledonian pine forest ecosystems

Introduction

The importance of understanding present day landscapes in the context of their long-term development has been increasingly recognised in recent years, as insight into past influences, processes and responses can provide a useful foundation for determining strategies for present and future conservation management (Green and Dolman, 1988; Birks, 1996; Tipping *et al.*, 1999). The overall aim of this thesis is to increase understanding of the long-term dynamics of an important and threatened ecosystem, the Caledonian pine forest. As most long-term processes operate outside the scale of a human lifetime, a combination of palaeoecological records and pollen dispersal modelling will be used. From around 4550 cal. BP (4000 BP), human activity is thought to have intensified (Tipping, 1994; Edwards and Whittington, 1997) and therefore this thesis will study both the period prior to this and the subsequent changes.

The area selected for study is Abernethy nature reserve (formerly Abernethy Forest), Inverness-shire, which, with its mosaic of pinewoods, bog and open heath habitats, provides a useful environment for studying long-term vegetation dynamics (Fig.1.1). Regional and local vegetation and fire histories are presented and a set of hypotheses are advanced that relate to processes such as climate change and human activity in the Caledonian pine forest ecosystem. These hypotheses are then tested using pollen modelling within the framework of a Geographical Information System (GIS) and used to generate scenarios for possible past landscapes at three time slices.

Each time slice is then presented visually as a 'palaeo-map', each map representing the most feasible scenario for spatial distribution of major vegetation units such as pine forest, birch woodland, bogs and open heath for a 15 km x 15 km study area (Fig.1.1). These maps are also considered as possible stages in the evolution of the current landscape and provide a basis for further discussion of concepts such as the 'naturalness' of Caledonian pine forest today and the effects of past and present environmental and management regimes. This chapter first reviews current understanding of the development of Caledonian pine forest during the Holocene, then more specifically long-term vegetation dynamics and current status of the site under

investigation, Abernethy nature reserve. Attention is drawn to areas where research is currently lacking, and the implications of this for future management are discussed. Several key areas for further research are identified, from which more specific thesis aims are defined. Finally, a site description and thesis outline are presented.

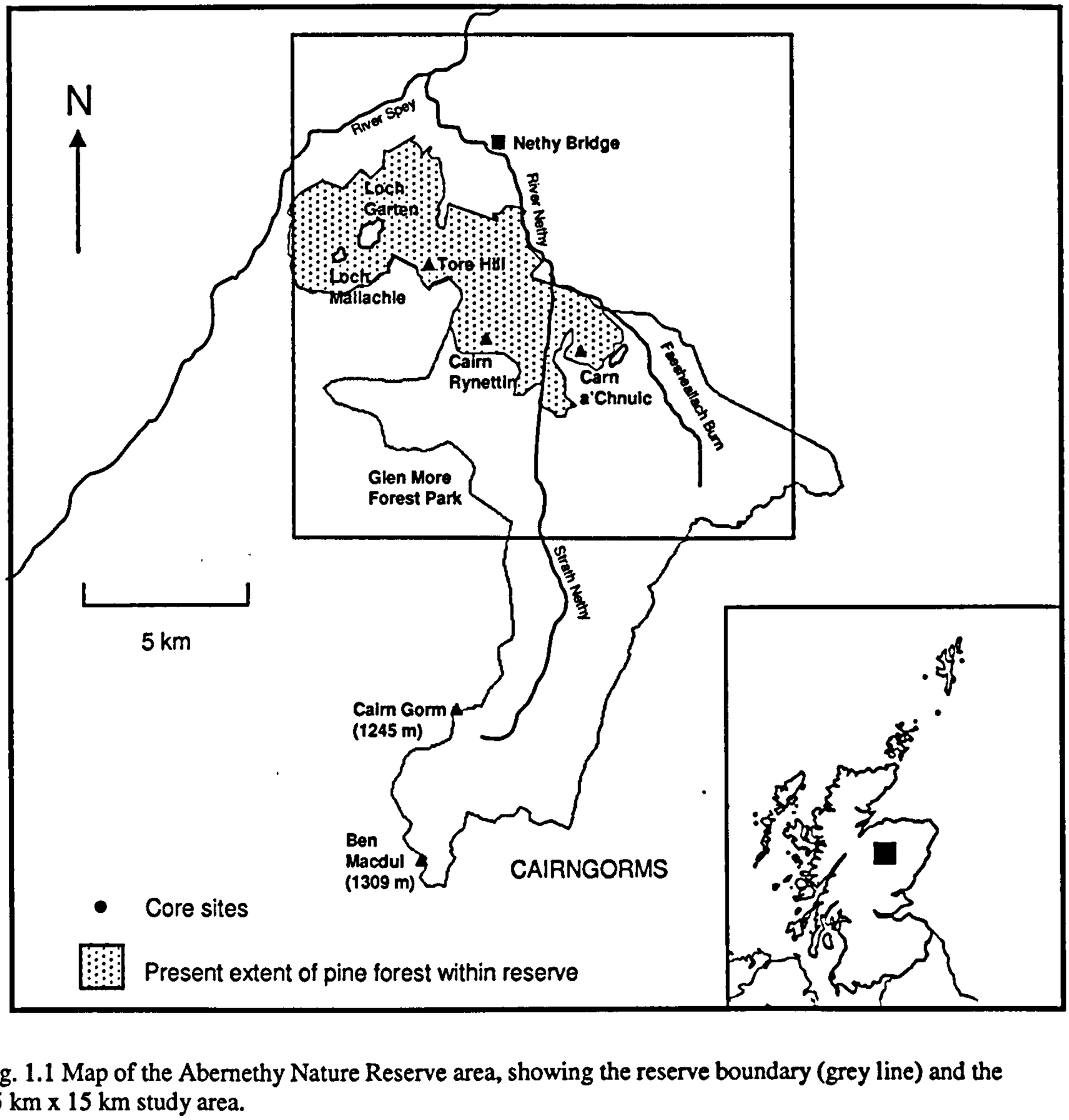


Fig. 1.1 Map of the Abernethy Nature Reserve area, showing the reserve boundary (grey line) and the 15 km x 15 km study area.

Fig. 1.2. Abernethy Forest: 15 km x 15 km study area showing locations mentioned in the text.

The importance of long-term vegetation dynamics

An understanding of long-term vegetation dynamics is fundamental for successful conservation management because many ecological processes and anthropogenic influences operate over long timescales (10^2 to 10^3 years). Whilst certain features of a landscape will be relatively constant over the long-term (*e.g.* geological and topographical features), ecological processes operate and interact across a range of timescales (Green and Dolman, 1988). Anthropogenic influences will also operate at a variety of timescales; some, such as burning, will constitute an abrupt but short-lived disturbance which may maintain one ecosystem type or cause temporary or long-term switches from one ecosystem type to another (Gill and Groves, 1981; Pyne, 1984). Other influences may have longer-lasting impacts, *e.g.* deer and sheep grazing, which have been identified as the major cause of suppressed woodland regeneration (Beaumont *et al.*, 1995). It is therefore difficult to assess the impact of such processes within a human lifetime using traditional ecological research methods. Without the long-term context, there is a danger that desired outcomes of current management will not be sustainable in the future, or that the timescales imposed for those outcomes will be unrealistic. Having a long-term context may also be useful guidance when considering which conservation goals are appropriate, because concepts of 'naturalness' are highly variable and have a strong cultural component (Peterken, 1996).

There is a pressing need to be able to assess not only the long-term effects of particular management strategies, but also how these effects may in turn be influenced by changing external conditions, such as increased precipitation or raised temperatures that may be associated with global climate change. With such changes believed to be taking place more rapidly than at previous points in history (IPCC, 2001), conservationists and land managers need to be aware of possible outcomes for a range of likely future scenarios to be able to plan the most effective long-term management strategies for the conservation of key habitats and species.

The development of predictive tools would be a useful contribution to conservation decision-making. Any conservation strategy will benefit some species and hinder others (Sutherland, 1995), so assessing the likely effects of future change on species and habitats of conservation importance is critical. Species of conservation concern tend to be those that exist close to their ecological limits and are thus more likely to be sensitive to long-term change. This thesis aims to

further the development of such a tool for an important and threatened ecosystem, the Caledonian pine forest. It demonstrates possible methods for quantitative reconstruction of past landscapes for selected time periods using traditional palaeoecological techniques combined with pollen dispersal and deposition modelling. Pollen dispersal modelling can now be used to test possible past scenarios against palaeoecological records for a landscape to produce more robust reconstructions. This can give an improved understanding of long-term dynamics which can be used to model the effects of future change, a technique which is well established in fields such as meteorology. This would enable feasible predictions to be made of the long-term effects of particular management interventions and external factors on a given landscape.

Caledonian pine forest has been selected for study because it is an important ecosystem for conservation as it provides habitats for many rare plant and animal species that occur nowhere else. On account of its marginal position in relation to the present day tree line, it could be expected to be particularly sensitive to climate changes, as appears to have been the case in the past (*e.g.* Blackford *et al.*, 1992). Caledonian pine forest is declining and fragmented, occupying only about 1% of its former range (JNCC, 1995) and the bogs within it are rare and sensitive habitats about which important management decisions need to be made (Legg *et al.*, 2001). This landscape provides a useful platform for the study of long-term vegetation dynamics because its peat bogs provide a rich palaeoecological archive. Also, for modelling and landscape reconstruction purposes, it is a relatively simple ecosystem with a low diversity of plant taxa occurring on the relatively infertile soils (JNCC, 1995).

Holocene vegetation dynamics in Scotland

The start of the Holocene, also known as the post-glacial period or Flandrian, covers the period from *c.*12,000 cal BP (10,000 BP) to the present day, following rapid climatic warming which began around 13,350 cal. BP (11,500 BP) (Bennett, 1984; Bowen, 1999). Early attempts to understand how vegetation developed in Scotland during the Holocene (*e.g.* Godwin, 1956; Durno, 1956, 1957) were based on undated pollen studies confined largely to coastal and lowland areas. Steven and Carlisle (1959) published a comprehensive review of the origins, history and ecology of the Scots pine *Pinus sylvestris* L. in Scotland. The palaeo-autecology and dynamics of *Pinus* have been particularly well researched, as long and detailed pollen and macrofossil records are available for the British Isles (*e.g.* Bennett, 1995). In addition, syntheses based on numerous dated pollen studies (*e.g.* Birks, 1989; Tipping, 1994) have allowed the main

events relating to the arrival and spread of other major arboreal taxa to be dated with some degree of confidence. However, there are still significant knowledge gaps in long-term vegetation dynamics for the later Holocene from 5600 cal. BP (5000 BP), due to the paucity of sites with secure chronologies (Tipping, 1994).

Following the disappearance of the last ice in Scotland at the end of the Loch Lomond stadial *c.* 12,250 cal. BP (10,200 BP) (Birks, 1989), pioneer grassland and tundra communities began to be replaced by scrub communities, probably dominated by juniper (*Juniperus communis* L.) and willow (*Salix* L.). These communities probably became increasingly fragmented by *c.* 11,850 cal. BP (10,000 BP) as birch (*Betula* L.) arrived almost synchronously across Scotland (Tipping, 1994). Between 10,500 and 10,400 cal. BP (9500-9000 BP), hazel (*Corylus avellana* L.) had spread rapidly across much of Scotland from possible refugia in the west (Birks, 1989; Tipping, 2003) and it appears to have had a fluctuating, competitive co-existence with *Betula* (Tipping, 2003).

The woodland at this time is thought to have been rather open with patches of bog and heath (Tipping, 1994; Gimingham, 2002), while lower altitudes would have been dominated by *Betula* and *Corylus* with smaller proportions of oak (*Quercus* L.) and elm (*Ulmus glabra* Huds.), which arrived from the south between 9500 and 9200 cal. BP (8500 and 8000 BP). It is unlikely that either *Quercus* or *Ulmus* became a significant component of the forest north of the Great Glen due to the hostility of the climate (Birks, 1989; Tipping, 2003) but *Quercus* appears to have become an important component of the woodlands of lowland Scotland by 6750 cal. BP (6000 BP) (Birks, 1989; Tipping, 1994).

From pollen records, it has been inferred that *Pinus* first appeared in Scotland around 10,400 cal. BP (Birks, 1989) although recent work on the presence of *Pinus* stomata in Glen Affric (Froyd and Bennett, 2006) has suggested a date around a thousand years earlier than this, a finding that could have major implications for understanding the immigration and spread of tree populations in the early Holocene. Evidence from differences in resin monoterpene chemistry in modern *Pinus* populations suggests at least two independent origins (Forrest, 1980; Kinloch *et al.*, 1986). There are several hypotheses regarding the mechanisms involved (Bennett, 1995) but it seems likely that *Pinus* colonised from one or more glacial refugia from the Loch Maree region in the north west of Scotland or from Ireland, and also from the continental mainland via England

(Forrest, 1992). Bennett (1995, 1996) suggested that by c. 9800 cal. BP (8800 BP) *Pinus* had spread from western Scotland and became the dominant forest tree across much of the Highlands, remaining so until *c.* 5000 cal. BP (4400 BP). In other parts of Scotland, *Pinus* was restricted in its range by competition from deciduous trees such as *Ulmus, Quercus* and *Corylus*, and subsequently (from 8400 cal. BP; 7500 BP) by alder (*Alnus glutinosa* L. Gaertn.).

Several palaeoecological studies of the *Pinus* tree line have important implications for the interpretation of pollen records in relation to both tree lines and the spread of tree taxa during the early Holocene. In the Kola Peninsula, northern Russia, Gervais *et al.* (2002) studied pollen, macrofossil and stomata evidence from a lake sequence. They concluded that *Pinus* had been present in the area as early as 9150 cal. BP (8150 BP), some 1000 years earlier than the date implied by the pollen record, when levels of *Pinus* pollen were as little as 4%. They suggested that these populations were restricted in population size and geographical extent, having become established via long distance seed transport. In northern Scotland, Froyd (2004) found *Pinus* stomata in bog sediments in East Glen Affric and was able to infer an earlier date for the first presence of *Pinus* than had been suggested by the pollen record. It may be that inferences from the pollen record concerning the timing of the spread and altitudinal and geographical range of *Pinus* in Scotland will need to be revised in future as further studies of this nature are carried out.

Alnus spread up the west coast and to central and eastern Scotland between *c.* 7800 and 6800 cal. BP (7000-6000 BP), occurring later (6400-5000 cal. BP; 5500-4400 BP) in northern, north eastern Scotland and upland areas (Tallantire, 1992) but colonising only to altitudes of 400 m (Birks, 1989). There are differing opinions as to the mechanisms of spread, with Smith (1970) suggesting that colonisation may have been facilitated by burning and clearance of *Alnus* (and possibly other tree and field layer species) by hunter gatherers. However, the evidence cited for this was the presence of microscopic charcoal on pollen slides, and, as Tallantire (1992) points out, inferring causal relationships from the coexistence of pollen and microscopic charcoal is questionable. It is not possible to ascertain the distance that fine, wind-blown charcoal particles may have travelled to the site and it is possible that such particles reflect a combination of many fire events, either natural or anthropogenic. Another view is that the spread of *Alnus* occurred in response to a period of more favourable conditions, *i.e.* increased wetness giving rise to greater amounts of suitable habitat, particularly in river valleys (Edwards and Ralston, 1984). However,

climatic conditions in upland central and eastern Scotland were not generally favourable to *Alnus*, which Birks (1989) and Tallantire (1992) suggest may explain its later spread to these areas.

Between 7800 and 5700 cal. BP, the forest is believed to have reached its maximum extent in Scotland, just before the onset of human disturbance (Bennett, 1984; Birks, 1988), and was likely to have been a diverse mix of *Pinus*, *Betula* and *Alnus* at lower levels, with other trees and shrubs such as *Salix* and *Juniperus* at higher levels (McVean and Ratcliffe, 1962). From *c.* 4400 to 3500 cal. BP (3900-3200 BP), there was a decline in tree abundance, particularly *Pinus*, and an increase in heather (*Calluna vulgaris* (L.) Hull) and herbaceous species (O'Sullivan, 1974; Bennett, 1995).

Evidence from pollen records and the remains of numerous tree stumps in northern Scotland has been interpreted as the beginnings of a widespread and severe decline in the geographical extent of *Pinus* and other tree species, which has been dated to 5000 cal. BP (4400 BP) or earlier. It is not yet possible to tell whether this truly reflects a change in the overall population or is related to a change in conditions making their preservation more likely (Fossitt, 1994; Bennett, 1995). Various hypotheses have been proposed for explaining the mechanisms behind such a 'pine decline', including increased wetness, anthropogenic factors, pathogen activity, changing fire frequency and soil deterioration (Birks, 1972, 1975, 1976; Dubois and Ferguson 1985; Gear and Huntley 1991; Bradshaw 1993; Bennett 1995).

Dubois and Ferguson (1985) examined evidence from hydrogen isotopes in cellulose from pine stump macrofossils and, for stumps from *c.* 4600 cal. BP (4000 BP), suggest that they were growing at a time of increased precipitation lasting from 4650 to 4350 cal. BP (4250-3870 BP). Although Pears (1988) and Tipping (1994) question their sampling strategy, calibration and application of the technique, there is strong evidence that climatic changes were severe enough to disrupt vegetation cover (Tipping, 1994). Blackford *et al.* (1992) suggest that changes in rainfall around 4600 cal. BP may have been connected to tephra deposits from Icelandic volcanoes, which would have increased the number of hygroscopic nuclei in the atmosphere. The ensuing increase in rainfall acidity may also have damaged trees already close to the limits of their ecological tolerance.

Radiocarbon dates from the many fossil stumps in the far north west of Scotland suggest that, prior to the decline, a short-lived advance of *Pinus* took place within a thousand years, between *c.* 5500 and 4200 cal. BP (4800 and *c.* 3800 BP) (Gear and Huntley, 1991; Huntley *et al.*, 1997). Furthermore, these trees were growing on blanket mire, although the low percentages of *Pinus* pollen found in the pollen records from these sites suggests cover was discontinuous, or that trees were growing close to their ecological limits. Since tree populations appear to have still been expanding in this way at the onset of their decline, Bennett (1995) proposes that human impact was unlikely to have been a major factor, particularly as there is no evidence for any change in anthropogenic pressures.

Bennett (1995) also suggests that there was no evidence for pathogen attack. Bradshaw's (1993) hypothesis states that *Pinus* decline was related to changes in fire regime, in that human clearance may have inhibited the burning cycle, allowing *Pinus* to be replaced by competitors. It is not possible to explore this further as there is little evidence relating to *Pinus* abundance and fire regime in Scotland (Bennett, 1995). Bennett (1995) suggests that variations in precipitation would lead to a spatially and temporally irregular pattern of decline, and Froyd and Bennett (2006) found no evidence of the phenomenon for pinewoods in East Glen Affric, supporting the idea that the pine decline across Scotland was neither synchronous nor ubiquitous.

It seems that complex and interdependent factors were involved in the vegetation changes around 5000 to 4600 cal. BP (4400 to 4000 BP), which also appear to coincide with the inception of blanket bog in large parts of the Atlantic coastal and upland regions of Britain and Scandinavia (Moore, 1975; MacKenzie, 2002). Moore (1975) proposed that human activity may have played a major role in blanket bog formation. He argued that Bronze Age forest clearance from topographically water shedding areas would be sufficient to increase the supply of ground water, with the absence of trees causing a reduction in both transpiration and interception. In northern Scotland, evidence suggests that *Pinus,* being close to the edge of its geographical range, was particularly sensitive to environmental changes (Blackford *et al.*, 1992; Lageard *et al.*, 1999).

It is difficult to evaluate the effects of human activity in the early to mid-Holocene as it is often invisible in the archaeological record and the few sites where evidence for agriculture has been found, *e.g.* 6350 cal. BP (5500 BP) at Balbridie on Deeside (Fairweather and Ralston, 1993), are

insufficient to allow any inferences about the scale of such activities to be made. It is likely that they took place on a sporadic basis at different locations, resulting in impacts at a scale too small to have been detected by most existing studies (Edwards and Ralston, 1984; Birks, 1988; Bennett, 1984; Tipping, 1994). Tipping (1994) argues that there are no unambiguous indicators of anthropogenic activity in the pollen record for Scotland in the early to mid-Holocene, as many 'cultural indicator herbs' (Behre, 1981) would have been naturally present to some extent if the forest were as open as suggested above.

Even less is known about vegetation dynamics of the past 5000 years, which Tipping (1994) attributes to a lack of securely dated palaeoecological records covering this period. There is some evidence of forest disturbance at Loch Garten *c.* 4200 cal. BP (3600 BP) which may have been linked to population influx (O'Sullivan, 1977). Smout (1997) argues that in the eastern Highlands, deforestation caused by a combination of farming practices and climatic deterioration from *c.* 4300 cal. BP (3800 BP) resulted in loss of most of the forest by 1000 cal. BP (1000 BP). From this he infers that often cited references to seventeenth and eighteenth century clearances for iron smelting, timber, deer, cattle and sheep are difficult to substantiate. An alternative view is that *Pinus/Betula* forests survived largely undisturbed in many areas until a subsequent phase of intensification of human activity that began *c.* 300 to 400 years ago (MacKenzie, 2002).

Breeze (1992) discusses how references to a 'Caledonian Forest' in historical documents dating from AD 77 (Pliny the Elder) may have been distorted into a 'great myth of Caledon' that has persisted until the present day. The assumption is that extensive pinewood was present across much of Scotland *c.* 2000 cal. BP (2000 BP). Whilst *Pinus* may have been the dominant tree in the eastern and central Highlands and parts of the north west, *Betula* and *Quercus* were important components of the native forest in the remainder of the Highlands, and remain so today (MacKenzie, 2002).

The most notable changes inferred from pollen records seem to be an increase in herbaceous taxa associated with open areas, and an increase in *Calluna*, but as already discussed, an increase in herbs cannot necessarily be linked to human activity (Edwards and Ralston, 1984). It is possible that more hospitable areas such as river valleys supported some form of agriculture and/or grazing which, if sustained, would lead to the irreversible development of heathland (Gimingham, 1972; Stevenson and Thompson, 1993; MacKenzie, 2002), whilst more marginal

upland areas continued to support hunter-gatherer activity (Edwards and Ralston, 1984). MacKenzie (2002) suggested that increases in *Calluna* and decline in *Betula* implied by pollen records in the Cairngorms show the nature and extent of landscape changes caused by pastoral activities from the Neolithic period onwards.

Vegetation dynamics in Caledonian pine forest

Caledonian pine forest is a priority natural habitat type under the European Community Habitats and Species Directive (JNCC, 2006a) and comprises relict, indigenous *Pinus* forest which is now restricted to the central and north eastern Scottish Highlands and some smaller areas in the western and Northwest Highlands. The forest has a mostly open canopy with a field layer usually dominated by ericaceous species and mosses. Other tree and shrub species include *Juniperus*, rowan (*Sorbus aucuparia* L.), downy birch (*Betula pubescens* Ehrh.), silver birch (*Betula pendula* Roth) and, to some extent, aspen (*Populus tremula* L.) and holly (*Ilex aquifolium* L.) (European Communities Commission, 1991). Interspersed with the semi-natural pine forest are areas of birch woodland. *Salix* and *Alnus* occur along watercourses, and *Alnus* is also locally frequent in stands of old, flushed woodland. *Salix* (mostly *S. aurita* L.) also occurs as moorland thickets (Scottish Natural Heritage, 2002).

The semi-natural habitats associated with the pine forest are important for many rare plants, birds, mammals, invertebrates and fungi, *e.g.* twinflower (*Linnaea borealis* L.), creeping lady's tresses (*Goodyera repens* L. (R.Br.)), capercaillie (*Tetrao urogallus*), Scottish crossbill (*Loxia scotica*), red squirrel (*Sciurus vulgaris*), wild cat (*Felis sylvestris*) and dragonflies such as *Coenagrion hastulatum* and *Somatochlora arctica* (Ratcliffe, 1977). The isolated and fragmentary nature of the present day forest increases the risks of further habitat loss and detrimental effects on species population dynamics (Forman, 1995). For successful conservation and restoration strategies to be developed, an understanding of the long-term dynamics of Caledonian pine forest is needed to provide a context within which to assess the likely impact of change in the future.

As outlined above, the initial decline of the native pine forest may have been a response to climate change leading to widespread blanket bog formation around 4600 cal. BP (4000 BP).

However, it is likely that human activities such as felling, grazing, burning and planting have since been a major influence on the subsequent development of the landscape, leading to reduced diversity and loss of extent of the remaining pine forest in recent times (Steven and Carlisle, 1959; O'Sullivan, 1977). It is possible that extraction of timber associated with the rise in industry in the sixteenth and seventeenth centuries resulted in the survival of forest in only the most inaccessible places (Carlisle, 1977), although as discussed above, Smout (1997) points out that this view should be regarded with caution . Extraction continued as recently as World Wars I and II, when large amounts of natural and planted *Pinus* were extracted and the decline continued into the late twentieth century, contributed to by intensive deer grazing (MacKenzie, 2002).

Although the role of fire is important for regeneration in pine forest and dwarf shrub heath ecosystems (McVean, 1963, 1964; Zackrisson, 1980; Pitkanen and Huttunen, 1999), it has been viewed as destructive and difficult to control (*e.g.* Booth, 1984) and, particularly over the past hundred years or so, active attempts have been made to suppress it (Proctor, 1998). This may have contributed to current regeneration problems and, although the use of fire in a conservation context has been controversial, there is now a more positive attitude towards examining the potential of prescribed fire for improving field layer diversity and *Pinus* regeneration (*sensu* Carlisle, 1977; Donnegan *et al.*, 2001).

Froyd (2006) has challenged the idea that the establishment or maintenance of *Pinus* in the Highlands of Scotland is related to fire history. Studies of pollen, macroscopic and microscopic charcoal from four lake sequences from Glen Affric, the Great Glen, the north west coast and eastern Sutherland showed that charcoal correlated well with concentrations of *Calluna* pollen, suggesting that fire was associated with the development of heath and blanket mire communities, not *Pinus* woodland. This is consistent with the findings of Odgaard (1992, 1993), who, using pollen and charcoal studies of heathland in Denmark, suggests that one of the main causes of forest destruction and heathland expansion and maintenance over the last 5000 years was frequent human-induced fire (inferred as anthropogenic from its correspondence with cultural indicator herbs).

Wooded bogs such as those which are found within the northern and western upland areas of Scotland (Gore, 1983) are an important component of forest and mire ecosystems in northern

Europe and boreal regions of Russia and North America, but are relatively rare in Britain and have received little attention until recently (*e.g.* MacKenzie and Worrell, 1995; Anderson and Harding, 2002; Legg *et al.*, 2001; McHaffie *et al.*, 2000, 2003). They are a UK Biodiversity Action Plan priority habitat for protection on account of their rareness and sensitivity to threats such as peat extraction, drainage, forestry operations and climate change (Legg et al., 2001; JNCC, 2006b), but, as yet, little is known of their origins and dynamics. Their present day ecology, like that of bogs in general, is not a reliable guide to their history because of significant changes in their dominant species, probably linked to climate change (Barber, 1993). Their present distribution pattern is not a reliable guide to their former distribution or abundance because they have been subject to human disturbance (Gore, 1983). Hence there are conflicting views as to whether wooded bogs represent a climax vegetation type, part of a bog-forest cycle that never attains a steady state, or a transient phase of secondary succession triggered by human disturbance (MacKenzie and Worrell, 1995). Where such a lack of consensus exists, there is a need to develop a better understanding of the status of the site as well as clear aims for any management decisions particularly when this may involve costly interventions, *e.g.* removal of trees from the bog surface or restoring the water table, such as those recently carried out under the EU LIFE project Wet Woods Restoration scheme SNH, 2002). Currently there is a lack of ecological information for these communities upon which to base such decisions (MacKenzie and Worrall, 1995).

Vegetation dynamics at Abernethy Forest: current knowledge

The palaeoecological studies carried out in Abernethy Forest during the 1970s (Birks, 1970; Birks and Mathewes, 1978; O'Sullivan, 1974) have provided a comprehensive history of regional post-glacial vegetation development. O'Sullivan (1973a) also studied relatively short-term, local heathland dynamics using mor humus profiles dating from *c.* 1500 cal. BP (1500 BP), which are discussed further in chapter 6. Evidence suggests that heathland formation began at different periods at different locations between AD 450 and AD 900, and that some currently forested areas had been open moorland until as recently as AD 1870. Analysis of sequences containing records from a longer time span would enable the development of heathland to be understood more fully. An attempt will therefore be made to use the pollen record to detect the onset of this apparent cycling of forest to heath and to suggest the timescale over which these changes took place.

There are important examples of wooded bogs at Abernethy Forest (Fig. 1.3) and some preliminary studies have been carried out which have classified these ecosystems on the basis of the growth form of the trees and the composition of the ground vegetation (MacKenzie and Worrell, 1995; McHaffie *et al.*, 2000; McHaffie *et al.*, 2003). As part of a wider study aimed at characterising bog pines in north east Scotland and assessing the stability or transience of wooded bogs, Anderson and Harding (2002) used cores from living trees to determine age for pines growing on bogs at Abernethy. They found that some *Pinus* growing on peat several metres deep were between 200 and 300 years old, but it was not possible to determine whether this arose as a result of natural processes or human interventions such as peat cutting.

Diversity and regeneration

It is likely that the forest was more diverse in the past and that the current scarcity of broadleaved species is related to a history of selective browsing or cutting (Summers *et al.*, 1997). *Pinus* regeneration at Abernethy appears to be hampered at present not only by a limited seed source, particularly in the heathland areas to the south and east of the current forest but also by the existence of a widespread heather (*Calluna vulgaris*) field layer (Hancock et al., 2005; Fig 1.4). In some less disturbed, older forest stands, the canopy species are more mixed and there is often a higher proportion of bilberry, or blaeberry (*Vaccinium myrtillus* L.) in the field layer, whilst other older stands are dominated by Pinus. *Vaccinium* also occurs in abundance within areas of Pinus plantations, but in c. 40% of the forest there is a *Calluna*-dominated field layer (RSPB, 2001). *Juniperus* is locally abundant around Loch Garten and Loch Mallachie and in sheltered areas such as the River Nethy valley and the north east facing slopes of Cairn Rynettin (Fig. 1.5).

The culling of deer since 1989 (Beaumont *et al.*, 1995) has encouraged *Pinus* regeneration, particularly in areas that are closer to seed sources and/or have a more open field layer structure (Fig. 1.6.). Experimental research into the effects of controlled burning, grazing and cutting on field layer and *Pinus* regeneration is also in progress to provide information about the effectiveness of such treatments as tools for improving tree regeneration and field layer diversity, particularly to increase the ratio of *Vaccinium* to *Calluna* (Servant *et al.*, 2003; Servant and Hancock, 2003).

Fig.1.3. Wooded bog near Duack Burn, northeast of Tore Hill, Abernethy Forest.

Fig. 1.4.Faesheallach Burn bisecting open heath on glacial deposits, looking northwest towards Abernethy Forest and the Spey valley.

Fig. 1.5. Juniper thicket with birch on east-facing slopes of Cairn Rynettin, Abernethy Forest.

Fig. 1.6. Regenerating pine forest near Memorial Hill, looking southeast towards the Cairngorms.

Fire history

Cavalho (1999) looked at charcoal as a proxy for fire history in 31 short peat monoliths, collecting one from within each National Grid kilometre square throughout the forested area of the reserve where peat to a depth of at least one metre was available. Although eight cores were found to have macroscopic charcoal, only two of these cores from near the north eastern tip of Loch a'Chnuic and due south of Carn a'Chnuic were analysed in any detail and there no independent dates were obtained. He suggests that fire has been an important disturbance factor at Abernethy Forest, decreasing in frequency in the recent past. A pilot study by McHaffie *et al.* (2000) analysed changes in pollen and macrofossils above and below a layer of large charcoal fragments from a soil pit excavated beneath mature pines growing on deep peat adjacent to Osprey Bog east of Loch Garten. A single peat profile was examined and the loss of *Sphagnum papillosum* remains above the charcoal was interpreted as a loss of bog vegetation. Also above the charcoal, an increase in the *Calluna* to *Pinus* pollen ratio was interpreted as open heath (*cf.* Iason and Hester, 1993) and local pine presence was inferred from the occurrence of pine needles and stomata within the peat (*cf.* Dunwiddie, 1987; Parshall, 1999). From this evidence, McHaffie *et al.* (2000) concluded that a forest fire event created a brief period of open heathland vegetation which was followed by development of closed canopy *Pinus* woodland. Fine resolution charcoal and pollen analyses are required to establish whether fire was the initial trigger for the change from bog to woodland.

Human impact

The earliest archaeological evidence for human activity in Abernethy Forest comes from the Neolithic, in the form of cairns (Wood, 1995) and traces of cultivation near Loch Garten (Smout, 1997). From a radiocarbon dated pollen study of a core from Loch Garten, O'Sullivan (1974) concluded from increases in percentage *Juniperus*, Coryloid and non-arboreal pollen that forest clearance around the loch began before *c.* 3900 cal. BP (3600 BP), perhaps in association with a population influx in the late Bronze Age. Lack of archaeological evidence, however, makes this difficult to substantiate (see chapter 6). O'Sullivan's (1973a) mor humus studies of heathland development over the past 1500 years were interpreted as evidence for burning, light grazing and deforestation, linked to farming practices between c. AD 400 and AD 1000.

The presence of peat cuttings, tracks and the remains of eighteenth and nineteenth century crofting activities, such as lime kilns, field systems and ruined dwellings, all indicate that human

impact has been a major factor in the long-term development of the Abernethy landscape over the past few hundred years (Summers, 2005). In addition, historical maps by Pont and Blaeu suggest that the Strathspey area was already well-populated and not extensively forested by *c.* AD 1600, indicated by the abundance of place names and fragmentary nature of the tree cover shown (Smout, 1997). It is not known for how long prior to this the area had been a well developed cultural landscape, and what impact this may have had on the forest. Historical records of commercial felling, burning and grazing date back to around 1728, although it is likely that smaller scale exploitation was taking place from a much earlier period (see chapter 5). Peak timber extraction took place around 1830 followed by a trend towards replanting from around 1840 (O'Sullivan, 1973b). Other impacts of commercial forestry include even-aged *Pinus* stands, timber extraction dams, ploughed areas and drainage ditches, although much restoration work has recently taken place (see site description).

Gaps in long-term vegetation dynamics research at Abernethy Forest

Stand scale dynamics

Abernethy is regarded as a classic site for the study of Holocene vegetation development but the long-term sequences studied so far reflect the vegetation at a broad, regional scale, so little is known about vegetation dynamics at the stand/multi-stand scale. Whilst it is believed that the forest was more diverse in the past, and pollen records suggest that *Betula* was more abundant until several hundred years ago (O'Sullivan, 1973a, 1974a), the extent to which the forest was structured as mixed *Pinus/Betula* stands or as *Pinus* stands with pockets of *Betula* and other broadleaved species is not known. Both types of stand occur today and it may be that one or both were more common in the recent past. It is difficult to study their long-term dynamics on the basis of their current status as they are now limited in their size and extent. Further understanding of the history of the mix of these stand types over the past 500 years is an important requirement for future forest management.

Past diversity

From increases in *Calluna* suggested by pollen records (e.g. O'Sullivan, 1974) it can be inferred that *Vaccinium myrtillus* has declined. The current distribution of *Juniperus communis* suggests human impact, as abrupt changes in abundance are seen. It is also scarce between the current forest edge and 650 m asl, above which it again becomes locally frequent. This suggests it

became locally extinct as the forest was lost. It is difficult to gain an idea of the past abundance of *Juniperus* and *Vaccinium* from the pollen record as both taxa constitute 'blind spots' in pollen analysis (*sensu* Prentice, 1986). *Vaccinium* pollen is insect dispersed and the efficiency of this mechanism means such taxa generally produce pollen in much smaller quantities than wind-dispersed taxa (Faegri and Iverson, 1989). Although *Juniperus* pollen is wind-dispersed, this taxon is dioecious so pollen productivity is variable and relatively low, and preservation is often poor, with grains frequently split or crumpled (Moore *et al.*, 1991). Also, it may have occurred as a non-flowering growth form in poor climatic conditions (Iverson, 1954), and evidence from modern pollen spectra from *Juniperus* communities in northern Britain supports the idea that growth form, as well as abundance in the vegetation, influences its representation in the pollen record (Birks, 1973).

It will be many years before the full impact of experimental burning, grazing and cutting treatments on tree regeneration and field layer composition and structure will be known, but results so far suggest that *Pinus* regeneration on *Calluna* moorland is improved following burning (Hancock et al., 2005).

Spatial pattern of human impact

Pollen studies that reflect the vegetation at a regional scale, such as those from Loch Garten and Abernethy Forest (Birks, 1970; Birks and Mathewes, 1978), are not suitable for detecting the smaller scale variations in landscape patterns that are associated with human impact (Birks, 1986). Other than O'Sullivan's (1973a) work on heathland development, little is known about the spatial pattern of human impact on the landscape, particularly for the period prior to the mid-eighteenth century. The extent of Mesolithic hunter-gatherer presence is difficult to assess due to a lack of recorded archaeological remains but field surveys around Abernethy and the Cairngorms region indicate that Neolithic and Early Bronze Age settlement remains may be more numerous and extensive than previously thought (Wordsworth, 2003; Turnbull Jeffrey Partnership, 1996). In the wider Abernethy landscape, there may be some pockets where relatively few changes have occurred and other areas that have been subject to frequent changes over time. Areas close to lochs and river valleys at lower altitudes would have been more favourable for hunter-gatherers in terms of accessibility, food and water supplies and shelter. The more exposed higher altitude areas to the south and east of the current reserve area would

probably have been less favoured, on account of inaccessibility and more severe winters (*cf.* Atterson and Ross, 2002).

Fire history

Little is known about fire frequency and rotation at Abernethy (Summers, 2005) and at both the regional and patch scale fire history is poorly understood, because no long-term charcoal records are available. MacKenzie and Worrell (1995) suggest that anthropogenic changes in fire frequency and severity may have had profound effects on wooded bogs in the past, killing *Sphagnum* and enriching the ground layer to allow regeneration of different vegetation communities. They considered natural fires to be sufficiently rare to allow recovery of the original vegetation to the pre-fire state before any subsequent fires occurred. Other than the pilot study by McHaffie *et al.* (2000), there is little evidence to support this. It is possible that fire and other processes, acting in different combinations at both local and forest-wide scales, were sufficient to cause changes in vegetation type, *e.g.* from open bog to woodland or from woodland to heathland.

Implications for forest management

One of the current management objectives at Abernethy nature reserve is to increase the extent of semi-natural pine forest by encouraging existing natural regeneration over all areas where trees are a potential natural component, including bogs, wet heath and dry heath (Taylor, 2000). Arguably, there is a need to develop more specific restoration models for a range of Caledonian pine forest habitats, to guide decision-making and indicate priorities for future research. Without research-based models for restoration, cultural perceptions may exert undue influence (Peterken, 1996) and goals may be set that are not realistic or achievable.

Where deliberate interventions are planned to restore areas of the forest that have lost their 'natural' character, consideration of the habitat requirements of target species is important, but, more often, detailed information concerning what comprises 'natural' is required. This may include more information about the scale and pattern of variations in woodland composition, *e.g.* the proportion of stands that should be mixed, and, within mixed stands, the amount of *Betula* or other broadleaved species that should be present.

It is important to have an idea of how open a 'natural' pine forest landscape should be, as a mainly forested landscape may not be 'natural' and therefore is not an appropriate or realistic management goal. If the reasons why forest cover has been lost are not understood and the locations from whence losses have occurred are not known, it is difficult to know how or where to channel what are often limited resources into actively encouraging regeneration.

Whilst monitoring of the effects of fire (and other treatments) upon field layer composition and structure provides valuable insight into the types of management prescriptions that may be suitable for the future (*e.g.* Servant and Hancock, 2003; Servant *et al.*, 2003), a long-term perspective can provide important additional information, particularly in relation to restoration of field layer composition that is sustainable in the long-term. This requires further knowledge of how the impact of fire is affected by fire return intervals (including frequency and length of any cycles) and how the characteristics of the vegetation being burnt may influence subsequent regeneration in the long-term.

Requirements for further research

Although Abernethy Forest is well researched in terms of general post glacial vegetation history, more information is needed about how external processes such as fire (both human induced and natural), clearing and grazing practices over the past few thousand years have shaped the current landscape mosaic. It would be useful to have a better understanding of the spatial pattern of human impact, including how these patterns have changed over time and what the main processes driving these changes were. Anthropogenic fire has probably had a major role in the development of the current landscape but even basic knowledge of fire and vegetation dynamics in Caledonian pine forest is lacking. An idea of the period of onset of the intensification of fire, and the occurrence of long-term cycling of fire events in relation to loss of forest and development of heathland, would be useful within the context of developing fire prescriptions for future management. This requires further study of heathland development to investigate change over a longer period than that since 1500 cal. BP (1500 BP).

It is clear that analysis of multiple sites representative of a range of landform types, altitudes, with different physical development and possibly different human exploitation histories, will enable the dynamics of the Caledonian pine forest ecosystem to be investigated. In particular,

there is a need to address gaps in knowledge for the period between the intensification of human activity and the onset of commercial exploitation.

Scale and scope of study

The concept of scale is important in both ecology and palaeoecology, as different patterns and processes are detectable at different scales (Weins, 1989). The scale at which a study is approached will determine the types of patterns that can be detected and types of processes that can investigated. It is therefore important to define the scale of the study clearly to ensure that the patterns observed are relevant to the scale of the processes under investigation (*e.g.* Webb *et al.*, 1978; Jacobson and Bradshaw, 1981; Birks, 1986).

Previous studies of long-term vegetation change at Abernethy Forest have been based on sediments from large lakes (*e.g.* Birks, 1970; Birks and Mathewes, 1978), so smaller sites than previously studied will be selected to reflect the surrounding landscape at a scale suitable for detecting more localised changes. At the kilometre scale, patterns relating to key processes that have contributed to changes in major landscape units can be investigated (Forman, 1995). Integrated macroscopic, microscopic charcoal and pollen records will be obtained to allow fire history and vegetation dynamics to be investigated at both regional and local scales. Changes in spatial patterns such as the distribution of major vegetation units, forest openness and forest composition and charcoal records should be detectable from pollen records. When considered with changes over time inferred from palaeoecological records, it will be possible to investigate processes such as changes in past diversity and forest openness, heathland formation, long-term fire history and the role of human activity at a finer spatial scale than has been achieved so far.

Aims and objectives

The overall aim for this thesis is to gain a better understanding of long-term vegetation dynamics in Caledonian pine forest. This will be achieved by determining, at a range of locations representing the diversity of the present day environment at Abernethy,

i) changes in forest openness and species composition
ii) spatial and temporal patterns in the development of heathland
iii) regional and local long-term fire histories
iv) evidence for the onset and intensification of human activity.

A secondary aim is to evaluate novel approaches to landscape reconstruction based on pollen dispersal modelling, and to use these in conjunction with palaeoecological records to identify feasible landscape reconstructions for past 'time slices'. This involves:

i) estimation of the spatial sensitivity of the modern pollen-vegetation relationship and assessment of the value of non-pollen palaeoecological indicators for identification of the main plant communities
ii) validation of a pollen dispersal and deposition model for Caledonian pine forest
iii) creating a range of possible past landscape scenarios for selected time slices
iv) Simulating pollen rain for those landscapes then comparing the simulated pollen with fossil pollen
v) Using dissimilarity measures to find the best fit landscapes for fossil pollen spectra for the selected time slices.

Site description

Abernethy nature reserve, Inverness-shire, covers around 13,000 ha and extends from the northern foothills of the Cairngorms into the Spey valley (Figs. 1.1 and 1.2). The site is currently owned and managed for conservation by the RSPB. The solid geology is predominantly Moine schists and gneisses, with a small area of granite near Loch Garten and Tore Hill. The drift geology comprises glacio-fluvial deposits of sand and gravel relating to late Devensian ice-sheet downwastage (Young, 1977). These drift deposits have been ice-sculpted, giving a gently undulating topography of kames, eskers and kettle holes that varies in altitude between 200 and 500 m above sea level, and it is on these deposits that the main forested part of the reserve is situated. The irregularity of the topography has led to the development of varied drainage patterns and hence a wide variety of plant communities (Ratcliffe, 1977). Steeper slopes occur where the River Nethy has cut down into these deposits, bisecting the reserve in an approximately south-north direction.

Three hills within the forested part of the reserve, Tore Hill, Cairn Rynettin and Carn a'Chnuic, rise to altitudes of 338 m, 474 m and 506 m respectively. Beyond the current forest limit,, summit altitudes in the Cairngorms are generally between 600 m and 1000 m, with the

southernmost tip of the reserve boundary extending to Ben Macdui (1309 m). There is a wide range of upland habitats including various examples of heath, mire and grassland. In the forested part of the reserve there are two large lochs, Loch Garten and Loch Mallachie; smaller lochans are more numerous in the higher ground to the south and east of the current forest limit.

The reserve contains one of the largest remaining fragments of semi-natural Caledonian pine forest in the UK, comprising 15% of the total remaining in Scotland (Summers *et al.*, 1997). The pinewoods are part of the Speyside-Deeside group of what was once an extensive tract of forest (Ratcliffe, 1977). Only around 2200 ha of a potential 6500 ha below the current presumed altitudinal tree line of *c.* 650 m (Summers, 2005) is classed as pinewood (National Vegetation Classification W18 *Pinus sylvestris-Hylocomium splendens* woodland), although there are a further 1150 ha of woodland of various types growing on mires. Within the pine forest there is good structural diversity in the age, form and height of trees, including the presence of a *Juniperus communis* shrub layer in many areas (Ratcliffe, 1977; Summers *et al.*, 1997). There are also some small areas of native broadleaved woodland, including stands of *Betula*, riverside *Alnus* woodland and pockets of aspen (*Populus tremula*) and rowan (*Sorbus aucuparia*) (Summers *et al.*, 1997).

Within the forest area, there are numerous oligotrophic to mesotrophic mires occupying valleys and former kettle holes (Ratcliffe, 1977), including two important examples of ombrotrophic raised bogs near Duack Burn, east of Loch Garten (Figs.1.2 and 1.3). Many of these comprise bog vegetation co-existing on a more or less permanent basis with open woodland or scattered, often stunted, trees (MacKenzie and Worrell, 1995). These and other wooded bogs are protected as examples of rare and sensitive habitats by the EC Habitats Directive on account of their European rarity and sensitivity to threats such as peat extraction, drainage, forestry operations and climate change (Legg *et al.*, 2001).

Human impact on the landscape is clearly apparent, particularly with regard to coniferous plantations and peat cutting. Whilst current RSPB policy is generally one of minimum intervention, considerable habitat restoration work has taken place in recent years, which includes clear felling of exotic plantations in the north of the forested area, restructuring Scots pine plantations and raising the water table on plantation-damaged bogs by blocking drains (McHaffie *et al.*, 2000). This has taken place as part of the EU Wet Woods LIFE project which

aims to enhance and restore favourable conditions on bog woodland sites that are candidates for designation as Special Areas of Conservation (Egret Consultancy, 1999).

Study area

Within the reserve, a study area was defined which would form the basis of the final landscape reconstruction. It was selected to include a range of landscape types, for example, the valley and basin mires of the northern forested part of the reserve, and open heath and blanket bog to the south and east. It was defined as a 15 km x 15 km square approximately centred on the RSPB reserve office at Forest Lodge (Figs. 1.1 and 1.2), within National Grid co-ordinates of 295000 to 310000 (Eastings) and 809000 to 824000 (Northings). Whilst all sampling took place within the reserve boundaries, the study area extends beyond the boundaries to provide a buffer zone to enable modelling of regional pollen dispersal and deposition around the sample locations, which are all located within a central 7 km x 7 km zone. In a northerly direction, the 15 km x 15 km study area extends to the Spey Valley, to Glenmore Forest Park to the south west, and into the northern flanks of the Cairngorms to the south east. The inner 7 km x 7 km area extends to Duack Burn north of Tore Hill to the north west, with samples located in an approximately north west to south east belt to just beyond Loch a'Chnuic in the south east.

Thesis outline

Chapter 2 details all methods used, including an explanation of the approaches taken, the rationale for selecting particular methods and the principles behind them. Chapter 3 is chiefly concerned with investigating modern pollen-vegetation relationships, including their spatial properties in relation to detecting forest openness and major vegetation units, and testing the usefulness of *Pinus* stomata as a tool for indicating the local presence of *Pinus*.

In chapter 4, the theoretical framework behind pollen dispersal modelling is outlined, followed by validation of the Prentice (1985) model for Caledonian pine forest using real vegetation data prepared from ground survey and satellite imagery using a GIS. Pollen loading is simulated for the landscape and simulated pollen counts are obtained for a set of sampling locations corresponding to the locations of a set of modern pollen samples. Simulated pollen counts are then compared with the surface sample data to assess model performance. Several schemes for

classifying the vegetation data at levels of complexity are tested to explore the maximum level of detail that could realistically be aimed for when applying the models to fossil pollen data for reconstruction purposes. The 'relevant source area of pollen' (*sensu* Sugita, 1994) for a range of hypothetical landscapes and opening sizes is also estimated to give an indication of the spatial sensitivity of the pollen signal and thereby aid decision-making about the eventual spacing of individual cores for palaeoecological reconstruction.

Chapter 5 presents two regional palaeoecological records from Abernethy Forest that record the rise to dominance of *Pinus sylvestris* in the early Holocene *c.* 7800 cal. BP (7000 BP). These are considered in the context of existing regional profiles for the area, incorporating new information from charcoal analysis to produce a new synthesis of long-term vegetation and fire history for the region. Trends in vegetation and fire history both before and during the period when human activity seems to have become a dominant influence over the ecosystem *c.* 4600 cal. BP (4000 BP) are discussed.

Chapter 6 focuses on the past 5000 years. Palaeoecological evidence for local to landscape-scale changes is analysed using five palaeoecological records from the Abernethy Forest reserve. At present these are correlated using synchronous horizons identified Holocene tephra deposits pending the outcome of a radiocarbon dating application. Changes in forest composition and openness, the long-term dynamics of heathland development and the long-term fire regime are all explored, and this chapter demonstrates the usefulness of using a network of multiple peat profiles for addressing these questions.

The findings from chapters 5 and 6 are then used in chapter 7, in conjunction with existing theories and knowledge of the region, to develop hypotheses for landscape change that could be tested using the fossil pollen record. Three broadly synchronous horizons were identified across the cores, for which possible landscapes arising from hypothesised processes of change were created, based chiefly on the physical characteristics of the landscape and the autecology of plant taxa. Pollen dispersal modelling was then used to simulate pollen for the coring locations, and the results statistically compared with the fossil assemblages to find the best fit and hence the most feasible landscapes.

Finally, chapter 8 considers the contribution that palaeoecology and pollen-dispersal modelling techniques can make to conservation decision-making and practice, and discusses the specific insights gained and implications for future management that arise from the results of this study. Strengths and limitations of the approach and future directions such work could take are also discussed.

Chapter 2. Methods

Introduction

In chapter 1, the need for long-term fire and vegetation history for Abernethy Forest was explained. In particular, there are gaps in knowledge for the period from just prior to the onset of greater human impact until the present day that need to be addressed. In this thesis, a better understanding of the long-term dynamics of the pine forest ecosystem will be obtained by investigating changes in forest openness and composition, heathland dynamics, regional and local fire histories and evidence for the onset and changes in human activity. A secondary aim is to assess the usefulness of pollen dispersal models for use with palaeoecological records to reconstruct past landscapes. This chapter discusses the approaches and methods chosen, the principles behind them, the rationale for their selection and how they relate to achieving the aims of the thesis. Details are also given of all procedures referred to in subsequent chapters.

Approaches to studying long-term vegetation dynamics

There are several main approaches to studying long-term vegetation dynamics: space-for-time substitution, long-term monitoring, historical and palaeoecological approaches. In space-for-time substitution, it is assumed that spatial heterogeneity of successional stages of modern plant communities across a landscape reflects the sequence of changes that would have occurred in the system following primary succession or disturbance (Pickett, 1989; Delcourt and Delcourt, 1991). A criticism of this is that it unrealistically assumes that sites of different ages have identical environments and ecological histories (Pickett, 1989).

The second approach, long-term monitoring, uses observations made from permanent plots or observation points that can be precisely relocated. It can be useful for revealing slow changes or the lasting effects of short-term events. However, it may be many years before useful results are available (Peterken, 1996). Thirdly, historical documents, such as estate records, can provide information on the status of the landscape over the past few hundred years, but such documents were often created for non-ecological purposes so they may lack detail and precision (Nielsen and Odgaard, 2004).

Finally, the palaeoecological approach uses methods that are based on analysis of sedimentary deposits with stable, continuous, datable deposition, and good preservation of pollen and other identifiable plant and animal remains (Birks and Birks, 1980; Lowe and Walker, 1997). It is based on the study of individuals, populations and communities of plants and animals that lived in the past, and of how they interacted and responded to environmental changes (Delcourt and Delcourt, 1991). It is often the only source of information about past ecosystem composition and function (Birks, 1996), especially where other approaches such as those outlined above become more difficult, *e.g.* in ecosystems that are dominated by long-lived taxa such as trees. Hence for this study, the palaeoecological approach was selected, as the changes under investigation are likely to have been infrequent, irregular or to have taken place over hundreds to thousands of years.

The palaeoecological approach

A useful aspect of the palaeoecological approach is that it is often possible to purposefully select the types of site that will provide the best data to answer the research questions (Webb *et al.*, 1978; Jacobson and Bradshaw, 1981; Jackson, 1994). This is because pollen deposited in different types of sediment (*e.g.* peat, lake sediment) and sizes of basin (*e.g.* large lake, small hollow) records the surrounding vegetation in different ways (Jacobson and Bradshaw, 1981; Birks, 1986; see also chapter 4). It was therefore important to define as far as possible for this study the scale at which the processes of interest (*e.g.* heathland development, changes in forest composition) would have operated, to ensure that the patterns observed in the palaeoecological records were relevant to the scale of the processes under investigation. The presence of numerous peat bogs within the Caledonian pine forest ecosystem provided a range of possible sites from which to collect suitable palaeoecological records.

Another useful aspect of the palaeoecological approach for long-term studies of vegetation dynamics is that it allows time-series analyses of multiple episodes of vegetation. Such studies are important in understanding whether vegetation changes are cyclic, vary in a systematic (and therefore predictable) way or are the result of random events (Shugart, 1984). Provided sediment has accumulated rapidly enough to record the effects of disturbance events on the vegetation and there is ecologically meaningful information, it should be possible to make inferences about return intervals and cycles for external processes such as fire or autogenic processes such as raised bog development (Delcourt and Delcourt, 1991).

Challenges in palaeoecology

One limitation of the palaeoecological approach is that the types of questions that can be effectively addressed are limited by the impossibility of establishing an experiment and replicating it, as effectively the experiment has already run (Deevey, 1969; Hurlbert, 1984). It is therefore necessary to look for evidence of past events then use this to test hypotheses that relate to presumed changes in the environment. There is no control over the environment as is possible in modern ecological studies.

Another challenge in palaeoecology is to find a means of interpreting the patterns in the record in terms of underlying causal processes (Birks, 1986; Delcourt and Delcourt, 1991). The future of palaeoecology as a discipline may rest on its being able to produce data in a form that can be meaningfully applied to issues of global relevance such as climate change and nature conservation (*e.g.* Davis, 1994). Its potential contribution to neo-ecology and conservation has been recognised over the past ten years or so (Birks, 1993, 1996; Davis, 1994; May, 1994; Delcourt and Delcourt, 1998), but not yet realised (see chapter 8).

Lack of replication at local and sites scales is also an issue in palaeoecology. Many studies, in particular those based on pollen analysis, have been based on the interpretation of single cores from sites that reflect the vegetation at a regional scale. Correlation with other regional profiles has allowed reconstruction of past vegetation for large parts of the British Isles. It has been argued that the degree of replication at the regional scale is excessive (Walker, 1990; Jackson, 1991; Birks, 1993) whilst there is a lack of replication at the local to extra-local scale that does not permit estimates of error or variability to be made (McConnell, 1996). A few studies using networks of multiple cores located a few kilometres apart have been carried out, but so far have mainly focused on investigating fine-scale temporal and spatial variability of the pollen signal and interpreting this in terms of fine-scale processes, rather than addressing problems associated with lack of replication (*e.g.* Davies and Tipping, 2004; Shaw and Tipping, 2006).

Using a range of records from the peat archive such as pollen, charcoal, volcanic ash deposits, testate amoebae and diatoms, palaeoecology can be used to address questions relating to key external processes, such as climate change, human impact, fire regimes and the effects of volcanic activity (*e.g.* Kuhry, 1997; Charman *et al.*, 1999; Barber *et al.*, 1999; Langdon *et al.* 2003; Lomas-Clarke and Barber, 2004; Blundell and Barber, 2005). However, multi-proxy

studies such as these are time-consuming, and, like fine resolution studies, the more proxies used, the fewer samples can be analysed overall.

Palaeoecology can also be used to investigate internal, or autogenic, processes such as raised bog development or hydroseral succession. Autogenic processes in bogs are recorded as a series of recognisable changes in stratigraphy, macrofossil assemblages and pollen records influenced predominantly by the plants themselves (Burrows, 1990). Stratigraphy and macrofossils can provide important information about the local presence of plants, whereas pollen studies can be designed to answer questions at a range of scales, from local to regional.

Approaches used in this study

In this thesis, long-term vegetation dynamics were studied by obtaining a set of palaeoecological records from a suite of peat cores, using pollen analysis as a major source of information. Pollen analysis is often regarded as the most successful palaeoecological method for investigating long-term changes in past vegetation and reconstructing Quaternary environments (e.g. Tipping, 1994; Lowe and Walker, 1997), as pollen reflects both spatial and temporal patterns in the surrounding vegetation. It provides a valuable means of investigating long term system processes and responses retrospectively, but there are three types of factor that make interpretation of fossil pollen assemblages difficult which relate to i) the formation of the assemblage (e.g. factors related to the plants themselves such as differences in pollen productivity and dispersal mechanisms), ii) post-depositional processes, and iii) errors introduced during sampling and analysis (Tipping, 1994). It is therefore of value to have a thorough understanding of the modern pollen-vegetation relationship derived from surface sample studies (*sensu* Davis, 1994).

Hence the initial part of the thesis uses surface samples to investigate the modern-pollen vegetation relationship (chapter 3) and assess the usefulness of pollen dispersal modelling for Caledonian pine forest (chapter 4). The use of modelling can, through improving the understanding of how a pollen assemblage reflects the surrounding vegetation, be a valuable tool for interpreting fossil pollen assemblages. The applicability of such models to the reconstruction of Caledonian pine forest landscapes is the subject of chapter 7.

For the palaeoecological part of the thesis, a network of small to medium sized basins were selected to allow investigation of the variability of fossil pollen and charcoal records at a smaller scale than that of previous work. The palaeoecological records were used to identify major patterns of change across the study area, which were used to develop hypotheses about past processes affecting landscape development. These hypotheses were in turn used to generate possible past landscape scenarios which were tested against empirical pollen records using pollen dispersal modelling.

The combination of palaeoecological techniques used was selected to provide information about past regional and local presence of plants, local presence of *Pinus* and an indication of the nature of the environment at the time of sediment deposition. Tephrochronology was chosen because tephra is particularly suited to the 'time slice' approach to landscape reconstruction, as it allows the identification of isochronous horizons. Macroscopic and microscopic charcoal were selected for analysis to provide information on both local and regional fires.

As many palaeoecological methods are by their nature time consuming, there is always a compromise between the number of sites that can be analysed and the number of samples that can be counted. This study attempted to move away from detailed analysis of a small number of sites to obtain a broader overview of regional and local landscape change, and the way in which the methods selected are applied reflect this approach. The remainder of this chapter presents the principles and rationale behind the methods themselves, and gives details of all procedures involved in field sampling, vegetation reconstruction, chronology and fire history.

Fieldwork

Site selection and sample collection: modern sampling

Modern pollen assemblages are useful for increasing understanding of the pollen-vegetation relationship. They are usually obtained by sampling lake sediments (*e.g.* Fossitt, 1994) or moss cushions (polsters) (*e.g.* Tinsley and Smith, 1974; Gaillard *et al.*, 1994; Hjelle, 1999). It is also possible to use surface litter and soils, but these are generally avoided because problems of differential preservation may introduce additional sources of error (*e.g.* Caseldine, 1981; Fall, 1994).

In this thesis, one purpose of the modern samples was to inform the interpretation of fossil pollen from peat sediments, so it was decided to use moss polsters as these are regarded as the most appropriate modern analogue for the interpretation of peat cores (Prentice, 1986). Prentice (1986) suggests that *Sphagnum* spp. should be used where possible, but previous work (Bradshaw, 1981; Boyd, 1986) suggests that moss species has no significant effect on pollen collecting properties so other perennial moss species were used where no *Sphagnum* was available. A second reason was that mosses have been found to provide the most accurate pollen representation of the surrounding vegetation, *e.g.* Wilmshurst and McGlone (2005) found that surface soils contain mostly corroded or reworked, resistant pollen types, and that lake sediments contain an amalgamation the types of pollen found in both soil and moss spectra. Thirdly, the environment provided by moss polsters is consistently moist and is also of suitable pH to preserve pollen well (Hall, 1989). Pollen impacting on grasses and herbaceous vegetation is subject to complex deposition and storage mechanisms (Caseldine, 1981), so these are considered unsuitable for surface sampling.

The length of accumulation time represented by the pollen in a moss polster is still subject to debate (*e.g.* Cundill, 1991; Hicks *et al.*, 1998). Until recently it has been assumed that the green parts of the *Sphagnum* polster hold a record of pollen accumulation covering several years, thereby minimising the effects of annual variability in pollen productivity between taxa (*e.g.* Bradshaw, 1981). However, Räsänen *et al.* (2004) compared pollen accumulation in moss polsters with that in adjacent Tauber traps and estimate that the length of accumulation time in a moss polster is between one and two years only, even where mosses were older than two years. In this case it was decided to sample from the green parts only to reduce problems of preservation (see Prentice, 1986), conducting sampling prior to the flowering season to minimise the effects of seasonal fluctuations in pollen production between taxa.

Data collection

Surface sampling took place in March 2003 (set L) and March 2004 (set SST) within the 15 km x 15 km study area described in chapter 1 (Fig.2.1). For set L, ten samples were taken using random co-ordinates from within each of 12 areas of relatively homogenous vegetation representative of a range of community types (see chapter 3), whilst the SST samples were taken from areas selected at random from a pre-defined belt transect selected to enclose varying

degrees of forest openness within the reserve (Fig. 2.1). At this time of year, potential weather

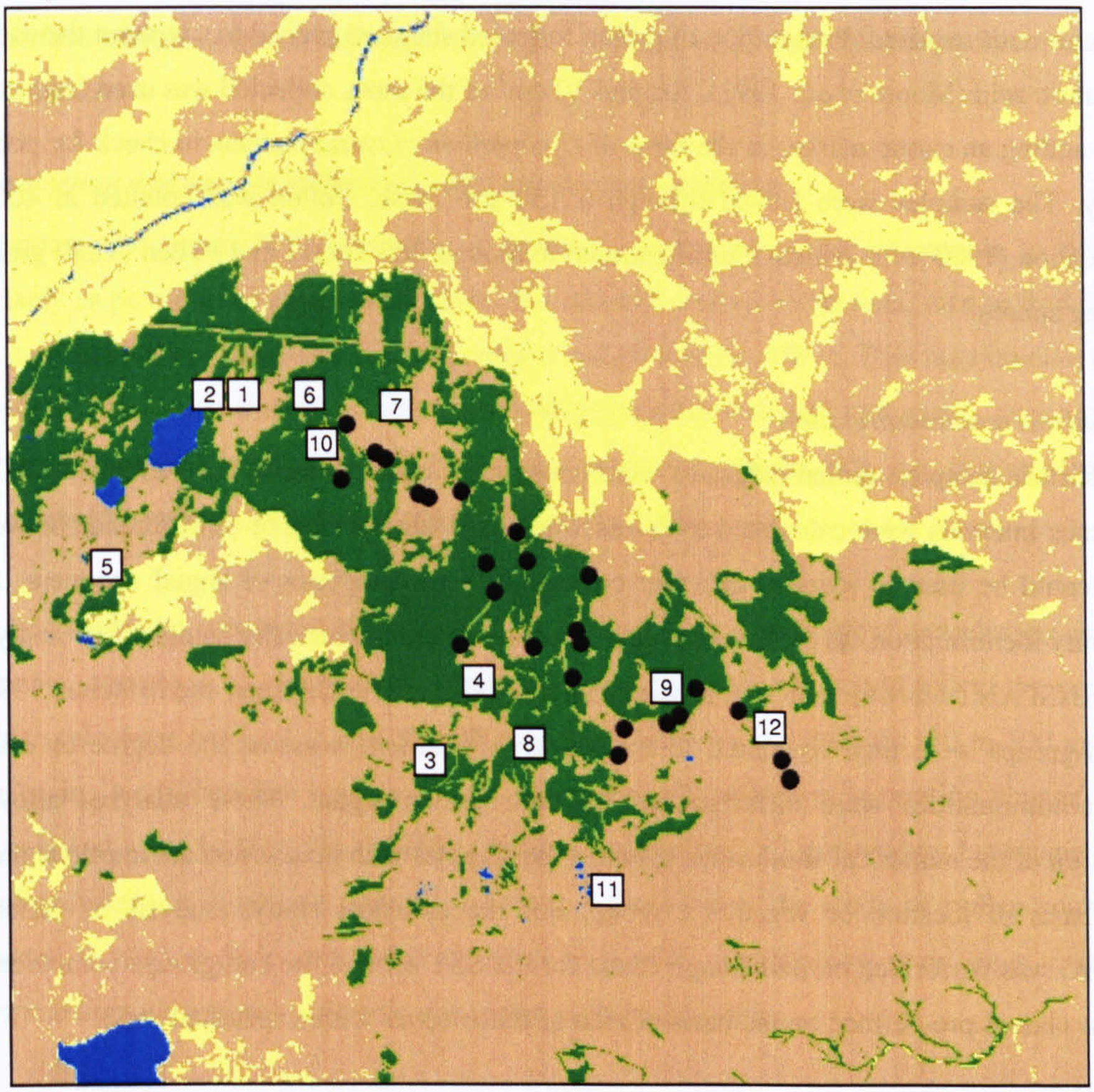


Fig. 2.1. Locations of surface samples from Abernethy Forest. See chapter 3, Table 3.1 for further description of the L sample locations.

constraints, disturbance to nesting birds and seasonal distortions to the pollen signal are minimised. Sample locations were geo-referenced using a handheld Garmin GPS and the surrounding vegetation was recorded (for further details see chapters 3 and 4). Individual L and SST samples were collected in the same way, with each sample being collected from a single

polster, using *Sphagnum* spp. where possible. Around 20 cm^3 of the green parts of the moss were snipped off from a 5 cm diameter circular area, before storing them in sealed polythene bags in a refrigerator until required. Preparation of pollen followed standard procedures without the use of hydrofluoric acid (Moore *et al.*, 1991). Around 10 cm^3 of the moss collected was used from each sample, adding an exotic marker in the form of *Lycopodium clavatum* tablets to check for pollen recovery. The samples were sieved through a 150 µm mesh. Pollen was counted at 400 x magnification (1000 x for critical identifications) to around 300 Total Land Pollen (TLP) grains, excluding spores.

Data analysis and interpretation

For all surface samples, pollen diagrams were constructed using *psimpoll* 4.10 (Bennett, 2002). Confidence intervals were calculated to assess whether or not the degree of difference between spectra could be used to identify different communities or categories of signal openness. For community identification, all set L assemblages were analysed numerically using cluster analysis and TWINSPAN (two-way indicator species analysis) (Hill, 1979; Oksanen and Minchin, 1997). The end-groups were then compared to the known vegetation to assess the degree to which different communities were differentiated by their pollen signal. These analyses allowed exploration of the numerical similarities between the samples with no *a priori* assumptions made on the basis of location or vegetation group. For the openness study, analysis of variance (ANOVA) was performed on percentage *Pinus* for the SST set and the end-groups compared to openness classes pre-defined on the basis of area of *Pinus* cover within specified radii.

For estimating the spatial sensitivity of the pollen signal, a sub-set of 53 samples from both the L and SST sets was used, having removed from the analysis set those L samples located under trees to reduce the possibility of a dominant local component in the pollen signal (*sensu* Jacobson and Bradshaw, 1981; Calcote, 1995). The modern pollen data were then compared with empirical vegetation data to estimate the area of the surrounding vegetation that the pollen sample was reflecting (*i.e.* pollen source area- see chapter 4), which was needed to give an indication of the spatial resolution possible and thus inform site selection for the palaeoecological sampling stage.

This subset of samples was also used to validate the Prentice (1985) model of pollen dispersal and deposition for Caledonian pine forest (chapter 4), as it was important to check that the model

was performing satisfactorily for major taxa before using it for landscape reconstruction. Validation involved using the model to simulate pollen assemblages for the same 53 locations as the surface samples, then comparing the results with the empirical pollen data to assess model performance.

Site selection and sample collection: palaeoecological sampling

A fundamental principle in designing a palaeoecological sampling strategy is to define as precisely as possible the research questions that are to be asked of the data, then to find the sites that can best answer those questions (Jacobson and Bradshaw, 1981). This may involve using a variety of basin sizes that reflect the surrounding vegetation at different scales, or a variety of sediment types that contain different types of palaeoecological records, *e.g.* diatoms from lake sediments for studying lake water quality (Battarbee, 1986).

For this study the processes of interest, such as heathland development and changes in forest openness, operate at an intermediate (landscape) scale, so sites that would reflect the vegetation at this scale were required. Large (> 100 m radius) and small to medium (30 m-100 m radius) peat basins were therefore chosen so that pollen records reflecting vegetation change at both regional and more local scales could be obtained to interpret the surrounding landscape. When deciding where to locate the network of sites, the results of the study of pollen source area (chapter 4) were used in an attempt to select sites with overlapping source areas to facilitate interpretation and reconstruction for the whole of the study area.

It was considered desirable to obtain at least one regional profile as this would allow cross-referencing with previous regional profiles from the area. Published regional signals have been based on lake sediments rather than bogs (*e.g.* Birks, 1970; Birks and Mathewes, 1978). Whereas differences in opening size between sites have in the past been largely ignored for the interpretation of pollen assemblages from smaller basins within heterogeneous landscapes, with an understanding of how pollen source area affects the pollen signal, it is now possible to make comparisons between sites. If pollen data can be supplemented by other palaeoecological records that can indicate changes in opening size (*e.g. Pinus* stomata and wood macrofossils indicating local presence of trees and possibly a reduction in opening size), this can allow inferences about changes in opening size to be made. As changes in openness were key to this thesis, it was also

considered important that the sites selected included examples where the present day vegetation is both forested and open to increase the likelihood of detecting past changes.

As fire history was also an important aspect of this thesis, peat sediments were selected rather than lake sediments, as they have been considered superior for analysis of charcoal, having a continuous record of airborne charred particle input with minimal post-depositional mixing and transport (Tolonen, 1986).

Field methods

The first step was to carry out an extensive auger survey to identify potential sites. The areas from which sites could be selected were restricted to those that were accessible and sufficiently distant from nesting bird species of concern. It was decided only to select from sites where at least 1 m of sediment had accumulated, to increase the possibility of obtaining a more complete palaeoecological record. Preference was also given to those sites within clearly defined topographical depressions (*e.g.* kettle holes), as these would have acted as foci for sediment accumulation and should have been less likely than more shallow or otherwise poorly defined basins to have had large fluctuations in the size of the bog surface, and hence the size of the canopy opening (assuming that the density of trees on bogs has always been less than that of the surrounding, better drained areas). Changes in canopy opening size can be problematic for the interpretation of pollen assemblages, as larger openings have larger pollen source areas (Jacobson and Bradshaw, 1981; Sugita, 1994; Bradshaw and Webb, 1985; see chapter 4). Care was taken to choose areas of apparently uncut peat which had no inflowing or outflowing streams.

Seven peat-filled basins were selected from within the 15 km x 15 km study area used for the modern sampling. These sites were distributed throughout the reserve and included closed canopy, open canopy and treeless blanket bog areas (see chapter 1, Fig. 1.1). Cores were extracted from the deepest parts of the basins using a 5 cm diameter x 1 m long Russian sampler (Belekopytov and Beresnevich, 1955; Jowsey, 1966), and peat stratigraphy was logged in the field using a modification of the Troels-Smith (1955) sediment description system (see below). The sections were then labelled, wrapped in plastic film and placed in plastic guttering for support before being refrigerated until required.

Vegetation reconstruction

In any heterogeneous landscape, basin size, vegetation pattern, species composition and vegetation structure are among the factors which will affect the spatial scale of the landscape reflected in the pollen records. For landscape reconstruction, it is important to be able to estimate the pollen source area as this will determine the lowest resolution at which the reconstruction can be carried out for the sites under consideration (Sugita *et al.*, 1999). Small forest hollows are dominated by local pollen so provide evidence of local vegetation, whereas large lakes are dominated by more distant pollen, so can only give broad information about the landscape and yield no information about the nearby surrounding plant communities (Jacobson and Bradshaw, 1981; Birks, 1993).

Bog sites are more difficult to interpret as they combine properties of the two, in that there will be a local component from the peat-forming plant communities (Evans and Moore, 1985; Bunting, 2002) and a regional 'background' component comprising many of the same taxa (Prentice, 1985; Bradshaw, 1994). In a study of non-arboreal moorland taxa, Bunting (2003) found that a large proportion of herb and dwarf shrub taxa is derived from source plants 5 m to 10 m away. The relative proportions of local to background pollen may also vary between taxa at the local scale (*e.g.* Hjelle, 1998). An understanding of pollen source area is therefore of crucial importance for vegetation reconstruction where bog sites are used. It is investigated for the study area with the aid of pollen dispersal modelling techniques in chapter 4.

Pollen analysis

An important aspect of this thesis was to test novel methods for vegetation reconstruction based on pollen dispersal modelling. This offers an alternative to the modern analogue technique, which is widely used in pollen analysis for interpretation of past assemblages using matches, or analogues, obtained from modern assemblages (see chapter 4). This technique would be difficult to use successfully in Caledonian pine forest because there are few modern analogues for communities such as *Betula/Corylus* woodland that are thought to have been widespread in the past (Tipping, 1994). Pollen analysis was used to obtain modern and fossil pollen data for model validation and landscape reconstruction (chapters 4 and 7). Pollen was also interpreted in the traditional way, using pollen percentage diagrams for cores from a network of sites to provide

information on long-term vegetation change throughout the study area (chapters 5 and 6). This allowed comparisons to be made with previously published pollen studies for the area.

Laboratory data collection

Samples for pollen were prepared using standard techniques (*e.g.* Moore *et al.*, 1991). *Lycopodium clavatum* tablets were added to known volumes of sediment (approximately 1 cm^3, measured by water displacement) to estimate pollen concentration. The spores are previously acetolysed so are distinguishable from any native *Lycopodium* spp. that may occur in the pollen sample (Birks and Birks, 1980). Samples were sieved through a 150 µm mesh and after acetolysis stained with safranin and mounted in silicon oil. Pollen was counted at 400 x magnification (1000 x for critical identifications), and identified with the aid of keys (Faegri and Iverson, 1989; Moore *et al.*, 1991; Beug, 2004) and the reference collection at the University of Hull. Unless otherwise stated, all pollen nomenclature follows that of Bennett (2005). Pollen percentage diagrams were constructed in *psimpoll* v.4.10 (Bennett, 2002).

Data analysis and interpretation

Analysis of error is important for assessing the reliability of results, making comparisons within or between sequences and identifying the main sources of error in the data collection or analysis process. However, despite the availability of the relevant statistical techniques, error analysis has largely been ignored in pollen analysis. The assumption has been that large counts (of the order of 500-1000 grains) will be sufficient to have confidence in the results (Bennett, 1994). However, this approach has perhaps contributed to the persistence of the 'detailed analysis of a few sites' approach (see Birks, 1996), as the time taken to count more pollen in each sample means that fewer samples can be counted overall. The advantage of counts over around 500 grains per sample is in revealing more rare taxa, rather than greatly reducing the overall amount of error (Maher, 1972; Birks and Line, 1992; Bennett, 1994).

As the aim of this study was to differentiate between broad vegetation communities based on the relative proportions of a few common taxa, such large counts were not deemed necessary, making it possible to analyse a greater number of sites. However, it was still important to establish whether or not smaller counts than are conventionally used are sufficient for this purpose. Calculation of confidence intervals indicated that a count of *c.*200±50 TLP would be sufficient for distinguishing broad vegetation communities (see chapter 3). The length of the

time period of interest (*c.* 5000 years) also required some compromise in the temporal resolution of samples (using depth as a proxy for time).The need for replication within the study area was seen as more important for the reconstruction than higher resolution temporal analyses, which would have meant fewer replicates.

A base sum of Total Land Pollen of trees, shrubs and herbs (TLP) was used, and where spores were present, their percentages were expressed as a percentage of Total Land Pollen and Spores (TLPS). Percentage pollen rather than pollen concentration data was used as the latter may be distorted by variations in the rate of sediment accumulation. Use of percentage data also allowed comparison with previously published work.

Analysis of the pollen percentage diagrams involved identification of regional and local zones to simplify the description process and facilitate comparisons between sites (chapters 5 and 6). Ratios of *Pinus* to *Betula* and *Calluna* were also calculated as an aid to interpretation, and for signals dominated by arboreal pollen, pollen concentration was used as a general indicator of increased tree presence. At the reconstruction stage, in order to identify the best matches for fossil assemblages from simulated pollen assemblages to the fossil pollen assemblages, dissimilarity coefficients were calculated, as used in the MAT (Overpeck *et al.*, 1985; see chapter 7).

Conifer stomata

Conifer stomata are lignified guard cells found on the underside of conifer needles and are increasingly used in palaeoecology. They make useful local indicators of local conifer presence, as needles tend to be deposited close to the point of origin (Clayden *et al.*, 1996). Being lignified, stomata are resistant to decay and survive well in lake and peat sediments long after the needles have decayed (Hansen, 1995).They are easily identifiable to genus or species using morphological characteristics (*e.g.* Hansen, 1995; Sweeney, 2004).

Compared with the number of fossil cores analysed for pollen, analyses including stomata are relatively few, but their usefulness as a tool in reconstructing tree lines has been recognised (*e.g.* Ammann and Wick, 1993; Clayden *et al.*, 1996; David, 1997; Froyd, 2004). In a surface study of lake sediments across a Siberian tree line, Clayden *et al.* (1996) found stomata occurred

consistently and abundantly in all sites with trees. Some species were better represented than others, and stomata were found in some treeless sites, which were attributed to long distance transport of leaf fragments or re-working of older lake sediments. Parshall (1999) evaluated the ability of modern pollen and stomata in closed canopy forest hollows to document stand-scale forest invasion in the Great Lakes. He found that conifer stomata corresponded closely with the presence of trees within 20 m, and also that the presence of needles and stomata were closely correlated, suggesting that stomata are a valid proxy for needle macrofossils.

There is clearly scope for further work to explore quantitative relationships between stomata and tree presence. Absence of stomata cannot be used to infer absence of the conifer and for presence of stomata to be taken as indicative of conifer presence, it is important to consider how needles may have reached the site. Bogs are potentially useful sites for further studies of stomata as needles (and other macrofossils) are unlikely to have travelled far and thus indicate that trees were present close by. For lakes, the possibility of needles having reached the basin by long distance water transport has to be considered, so presence of stomata in lake sediments is not necessarily indicative of tree presence in the immediate surrounding area.

For a study such as this where establishing the local presence of trees is of importance, the use of stomata or wood and needle macrofossils was deemed an essential complement to pollen analysis. It was decided to use stomata as an aid to detecting local tree presence as this is a potentially important indicator for a decrease in opening size (and therefore pollen source area), which has implications for the interpretation of the pollen signal.

Laboratory data collection

Stomata are of a similar size and chemical resistance to pollen grains (MacDonald, 2001) so no additional preparation besides that used for pollen was required. The total number of *Pinus* stomata observed during the pollen count for each sample was recorded, using the stomata keys of Hansen (1995) and Sweeney (2004) to confirm identification.

Data analysis and interpretation

As stomata are typically found at low abundance relative to pollen (MacDonald, 2001) they were presented on a simple presence/absence basis. No inferences about *Pinus* abundance were made and absence was not interpreted as absence of *Pinus*. *Pinus* stomata presence or absence in the

surface sample data was compared with vegetation data categorised by distance from *Pinus* to gain an indication of the strength of association with local tree presence (chapter 3). The use of bog sediments, rather than lakes, reduced the possibility of misinterpreting stomata from needles transported in from long distances as local presence.

Peat stratigraphy

Peat bog development is a largely autogenic process once it has begun, *i.e.* influences on plant growth are from the plants themselves rather than external factors. It is therefore possible to trace bog development by looking at the changes in stratigraphy (Burrows, 1990). The composition of the layers can provide useful clues about the plants that were growing at the time of accumulation, and if plant remains can be identified, changes in species composition can be used to infer long-term changes. Peat stratigraphy can also be used to infer changes in the local depositional environment, *e.g.* a change from fine lake muds to fibrous peat or wood peat followed by *Sphagnum* peat may represent the process of basin infilling, as a lake is colonised by fen species, trees and finally, as the level of the water table is exceeded by the bog surface, *Sphagnum* mosses (Burrows, 1990).

It is a useful complement to pollen and stomata analysis to describe the stratigraphy of each core. Information on depositional environment or plant composition can be used to make inferences about basin type and size that may have relevance for the interpretation of pollen data, in terms of the likely taxa present in the local pollen component or the size of the pollen source area.

Data collection

Sediment units were first logged in the field and then checked in the laboratory using a modified version of Troels-Smith's (1955) system (Aaby and Berglund, 1986; Table 2.1). This is a descriptive approach that is based on the assumption that all sediments are mixtures of components. The proportion of each component is recorded on a five point scale (0-4) so that the total of components is always four. The degree of humification was estimated using a five point scale (Table 2.2).

Table 2.1. The Troels-Smith sediment classification system, modified from Troels-Smith (1955) and Aaby and Berglund (1986). Sediment types shown in the key are those used in pollen diagrams in chapters 4 and 5. Patterns are combined on the diagrams at densities of 1 to 4 (to a total of 4) depending on their relative proportions in the sediment, but for clarity are shown separately at density 2.

Class	Symbol	Element	Description
	Sh	Substantia humosa	Humous substance, homogeneous microscopic structure.
Turfa (peat)	Tb $^{0-4}$	T. bryophytica	Mosses, +/- humous substance.
	Tl $^{0-4}$	T. lignosa	Stumps, roots, intertwined rootlets, of woody plants -/- trunks, stems, branches, etc., connected with these. +/- humous substance.
	Th $^{0-4}$	T. herbacea	Roots, intertwined rootlets, rhizomes, of herbaceous plants +/- stems, leaves, etc., connected with these. +/- humous substance.
Detritus	Dl	D. lignosus	Fragments of woody plants > 2mm.
	Dh	D. herbosus	Fragments of herbaceous plants > 2mm.
	Dg	D. granosus	Fragments of woody and herbaceous plants and sometimes of animal fossils < 2 mm > ca. 0.1 mm.
Limus (mud)	Ld $^{0-4}$	L. detrituosus	Plants and animals or fragments of these; particles < ca. 0.1 mm. +/- humous substance.
	Lso	L. siliceous organogenes	Diatoms, needles of sponges, siliceous skeletons, etc., of organic origin, or parts of these. Particles < ca. 0.1 mm.
	Lc	L. calcareus	Marl: not hardened like calcareous tufa. Particles < ca. 0.1 mm.
	Lf	L. ferrugineus	Iron oxide. Particles < ca. 0.1 mm.
Argilla	As	Clay	Mineral particles < 0.002 mm.
	Ag	Silt	Mineral particles 0.002 to 0.06 mm.
Grana	Ga	Fine sand	Mineral particles 0.06 to 0.6 mm.
	Gs	Coarse sand	Mineral particles 0.6 to 2 mm.
	Gg	Gravel	Mineral particles > 2 mm.

Key:

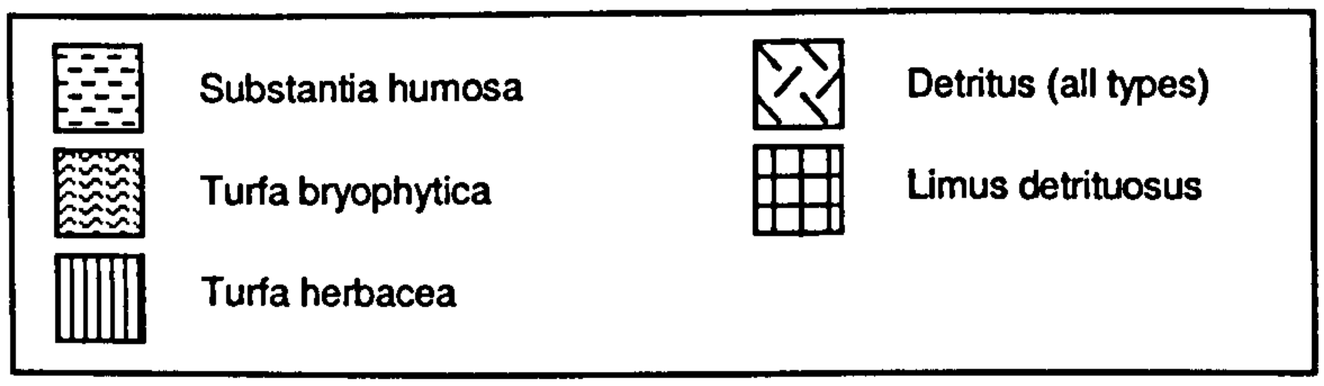


Table 2.2. Humification index modified from the Troels-Smith (1955) system.

Degree of humification	Sediment description
0	Fresh plant material, colourless water on squeezing
1	Plant material well preserved, dark coloured water on squeezing, 25% through fingers
2	Plant material distinct but partly decayed, 50% through fingers
3	Plant material decayed, indistinct, 75% through fingers
4	Plant material barely visible or absent, 100% through fingers

Traces of additional components not exceeding one eighth of the total are indicated using a plus sign (see Table 2.1). Sediment composition was added to all pollen diagrams using *psimpoll* v.4.10 (Bennett, 2002). The length of the profile and stratigraphy were used to determine core sampling intervals and depths, ensuring that all sedimentary units were represented in the pollen and charcoal analyses.

Calibration of the pollen-vegetation relationship and model validation

As already discussed, reconstructions of past landscapes can be greatly improved if pollen analysis is based on a thorough understanding of the pollen-vegetation relationship. This can be studied both theoretically and empirically using modern pollen in conjunction with data on the surrounding vegetation and the insights gained have contributed to the development and validation of models of pollen dispersal and deposition that can be used in quantitative reconstruction of past vegetation. In this thesis modern pollen samples are used to validate the Prentice (1985) model of pollen dispersal which is then used in the reconstruction process (chapters 4 and 7).

Detecting human activity in the pollen record

Cultural development and the introduction of new technologies, particularly since the Neolithic (*c.* 4600 cal. BP; 4000 BP), allowed humans to exploit the natural environment at a scale unprecedented during the Holocene, which resulted in the deflection or prevention of vegetation change or the introduction of entirely new variants (Walker and Singh, 1993). The impact of human activity on an ecosystem to a large extent depends on the sensitivity of that ecosystem, but in upland landscapes such as Caledonian pine forest, it would be expected that human activity would have involved substantial forest clearance for agriculture and grazing. In the South Pennines, Tallis and Switsur (1990) interpreted fluctuating non-arboreal pollen levels and abundant charcoal as evidence that tree line scrub communities were more prone to disturbance than lower woodlands. Disturbance was in part attributed to Mesolithic burning and grazing practices between 10,100 and 4450 cal. BP (9000-4000 BP). Such processes may also have operated at the tree line in Caledonian pine forest as early as the Mesolithic, climate notwithstanding.

Using the presence of particular pollen taxa as indicator species for human activity (*e.g.* open conditions associated with sustained grazing) assumes a thorough knowledge of factors affecting the distribution of the plant species in question. Behre (1981) assessed the value of a number of 'cultural indicator' herbs. Pollen from cultivated crops was regarded as the best indicator, but within the *Hordeum* group, pollen of cultivated species (*e.g.* barley, *Hordeum vulgare*) cannot be reliably distinguished from that of wild grasses (Andersen, 1979). Similarly, many other crop plants can only be identified to a taxonomic level that also includes their wild counterparts (*e.g.* Brassicaceae). *Plantago lanceolata* is regarded as the classic anthropogenic indicator for pasture (Behre, 1981; Moore *et al.*, 1991), but where farming economies were different from those seen today it may be more difficult to interpret. Light levels in wood pasture may have been inadequate to support *Plantago lanceolata*, and it has also been shown to occur at low levels in pollen samples not taken from areas in close proximity to grazing (Tinsley and Smith, 1974; Bunting, 2003).

Rumex is also considered potentially useful indicator of human activity, although some species can occur in association with natural communities, particularly in fen peats (Behre, 1981). Indicators of nitrogen-rich conditions include *Urtica,* Chenopodiaceae and *Artemisia.* Whilst the level of taxonomic precision possible for these taxa does not allow them to be differentiated

from those taxa occurring naturally in coastal communities (Behre, 1981), they may be useful indicators for the effects of grazing, settlement or agriculture in Caledonian pine forest.

Tipping (1994) argues that there are no indisputable indicators of human activity for pollen records from Caledonian pine forest, as many 'cultural indicator' herbs (Behre, 1981) occur naturally, particularly as it is likely that conditions were always at least partially open. Human activity can be inferred from the presence of unprecedented changes in the pollen record, *i.e.* at a rate or level not observed under natural conditions (Walker and Singh, 1993). Typically this includes an increase in percentage herb pollen and a decline in percentage tree pollen (Edwards and Whittington, 1997).

Tephrochronology

The occurrence in peat deposits of volcanic glass, or tephra, from Holocene eruptions in Iceland was first identified in Scotland by Dugmore (1989). These microscopic shards are an important tool for investigating vegetation dynamics, as they allow time-parallel marker horizons, or isochrones, to be identified. A number of studies in Britain and Ireland have since located numerous tephra layers (e.g. Hall et al., 1994; Hall, 1998; Newnham and Lowe, 1999; Hall and Pilcher, 2002; Langdon and Barber, 2004), from which at least seven isochrones for Scotland have been dated, using either radiocarbon dating of contemporary peat deposits, or their stratigraphic position within a dated profile (Dugmore *et al.*, 1995). Of these, one of the best dated is the Hekla-4 layer, which has been dated to *c.* 4260 cal. BP (3830 BP) on the basis of at least 27 sites in the UK and Iceland (see Dugmore *et al.*, 1995).

It was decided to use tephra as a means of identifying 'time slices' for the landscape reconstruction. On the basis of previous studies where tephra has been found in the Abernethy Forest area (Langdon and Barber, 2004; Blundell and Barber, 2005) it was considered likely that tephra would be found within the study area. However, the location of tephra may not necessarily coincide with changes in the palaeoecological record for which dates would be useful, so the acquisition of radiocarbon dates for key events inferred by the pollen and charcoal profiles is considered a priority for future work. Meanwhile, a provisional chronology is obtained by comparing pollen assemblage zones and distinctive changes in pollen proportions

(*e.g.* the first increases in percentage *Pinus* and *Alnus* pollen) with corresponding changes for existing dated profiles for the reserve (*e.g.* Birks and Mathewes, 1978).

Data collection

Holocene tephras in the British Isles generally occur at low concentrations of 5 to 50 shards per cm^3 and being in the size range of 10 μm to 100 μm cannot be visually identified within peat (Dugmore, 1989). Hence, to locate tephra in the first instance, an ashing technique was used, based on that of Pilcher and Hall (1992). Contiguous 8 cm or 10 cm sections of each core (around 2 cm^3 per sample) were burned off at 600°C for 3 hours. The remaining ash for each sample was suspended in glycerol jelly, mounted on a microscope slide and 50 mineral particles were counted at 400 x magnification under a light microscope, inclusive of any tephra located. Tephra shards were identified by their morphology and highly vesicular appearance (*cf.* Dugmore, Larsen and Newton, 1995). For samples where tephra was present, the appropriate part of the core was re-sampled in contiguous 1 cm sections and the preparation and counting procedure repeated to locate the peak concentration. This depth was identified as the location of the isochrone.

Shards were then subjected to geochemical analysis using an electron microprobe. The ashing technique is not suitable for preparing tephra for geochemical analysis because the alkali content of the samples is altered at temperatures above 350°C (Dugmore *et al.*, 1992). A peat sample of around 5 cm^3 was prepared using the acid digestion technique described by Dugmore (1989) and Dugmore *et al.* (1995). The residues were mounted in epoxy resin onto frosted glass slides then polished using six micron and one micron diamond pastes in succession to expose the shards. The samples were carbon-coated for analysis at the Tephrochronological Analytical Unit at Edinburgh and examined using a Cameca SX 100 electron microprobe at an acceleration voltage of 20kV and a beam current of 4nA measured across a Faraday cup. A spot beam was defocused to 10μm to reduce the problem of sodium mobility and prior to each session the instrument was calibrated for 10 major elements typically found in high silica volcanic glasses using a series of standards of known composition (see Dugmore et al., 1995).

Data analysis and interpretation

A minimum of ten single shards with analytical totals of at least 95% were analysed from each sample, and in line with previously published data, the results were not normalised, as it has been recognised that the degree of error increases progressively through the analysis and a more effective correction process is needed (Dugmore *et al.*, 1995). Identification was carried out by comparing the proportions of calcium and magnesium oxides against those of representative type material of known geochemistry and age (*e.g.* Dugmore *et al.*, 1995).

Charcoal analysis

Since the 1960s, analysis of charcoal has been used in palaeoecological studies, particularly in relation to prehistoric human activity and modification of vegetation by fire (Tolonen, 1986; Blackford, 2000). Although it is not possible to distinguish natural from anthropogenic fire (Scott *et al.*, 2000), it is often possible to infer human activity from increased fire frequency and/or continuity in the charcoal record (*e.g.* Innes and Simmons, 2000; Moore, 2000).

For communities such as pine forest, heath and blanket mire, where fire undoubtedly plays an important role and helps to maintain diversity (Pitkanen and Huttunen, 1999), charcoal analysis has been used to investigate vegetation development (*e.g.* Caseldine and Hatton, 1993; Stevenson and Rhodes, 2000). However, in Scotland the potential of this technique has generally been applied to detecting human activity only a small number of ecological studies of the role of fire have so far been carried out (*e.g.* Froyd, 2006).

Charcoal preserved in peat and lake sediments provides a proxy record of past fire history, and the categories of factors that make interpretation difficult are similar to those for pollen, *i.e.* processes of production, dispersal, deposition and extraction from the sedimentary environment. However, there are additional factors, in that charcoal occurs across a wide range of particle sizes (Tolonen, 1986) and fire events are much more unpredictable in time and space. Depending on their size, type and duration, fires can release large and often hugely varying amounts of charcoal (Patterson *et al.*, 1987). Such challenges have inevitably hampered the development of quantitative tools for interpretation of fire events and particular challenges remain for determining particle source area and exploring the effects of post-depositional processes (Whitlock and Larsen, 2001).

Several reviews comparing different methods have been published (Patterson *et al.*, 1987; Figueiral and Mosbrugger, 2000; Whitlock and Larsen, 2001) and there are also several studies comparing the results of different methods of analysis and interpretation (*e.g.* Blackford, 2000; Kangur, 2005). These should assist further progress towards developing standard methods for the quantification and interpretation of charcoal, which should make comparisons between studies easier in the future than they are at present

a) Microscopic charcoal

The presence of microscopic charcoal is a good general indicator of periods of burning at a regional scale, as it is present whether or not there is macro-charcoal indicative of local fire. Even with non-contiguous sampling as is often associated with charcoal counted from pollen slides, it can give an indication of general trends in past burning (Whitlock and Larsen, 2001). Innes and Simmons (2000) propose that its presence or absence and relative frequency in a sediment profile may allow inferences on the intensity, frequency and locations of fires to be made. However, as the signal contains components that are from different origins, and microscopic charcoal is probably both local and regional in origin, they suggest that exact quantification is not always informative, and it may be more realistic to regard charcoal abundance as a relative, general indicator of fire activity at the time.

There is still a lack of consensus on how microscopic charcoal should be interpreted, *e.g.* Patterson *et al.* (1987) suggested it can be a sensitive indicator of natural and cultural environmental change. Clark (1988a) proposed that poor correlations between local fires and charcoal from pollen slides can be explained by such charcoal being largely extra-local in origin.

b) Macroscopic charcoal

Although microscopic charcoal will increase during a local fire it is not possible to reliably determine its source area (Simmons and Innes, 2000). Hence an estimate of macroscopic charcoal abundance is more useful to establish whether or not the fire is local (Whitlock and Larsen, 2001). A number of studies based on modern data (Larsen and Macdonald, 1998; Blackford, 2000; Ohlson and Tryterud, 2000) have demonstrated that the presence of macroscopic charcoal fragments is associated with *in-situ* fire. The range of size classes seen appears to vary depending on the structure and composition of the vegetation prior to burning, as

well as with the characteristics of the fire event itself. Some attempts have been made to explore this experimentally, *e.g.*, Ohlson and Tryterud (2000) quantified macroscopic charcoal from a range of size classes captured in traps within and around experimental forest fires. They concluded that the presence of particles >= 0.5 mm is a reliable indicator of local fire influence. However, the absence of such particles was treated with caution as, possibly due to differences in fuel characteristics, this could not be taken as an indicator of the absence of local fire.

The idea that macroscopic charcoal particles are *in situ* indicators of local fires is also supported by Blackford's (2000) study of an uncontrolled heathland fire. He found clear, non-overlapping differences in the number of fragments >125 μm from transects across burned and unburned areas, and concluded that charcoal abundance was sufficient to be maintained as a 'charcoal peak' following subsequent sediment accumulation. Whitlock and Larsen (2001) suggested that a typical local fire event is represented by >50 particles per cm^3 in the 125μm to 250 μm size class, with a non-local fire event showing few or no particles in this size class.

Macroscopic charcoal can also be used as a source of palaeobotanical information if fragments are large enough to allow identification to species level. It can then be a useful supplement to the analysis of pollen, macrofossils and stomata when attempting to discern local presence of plants. The technique has been more fully exploited in archaeology than palaeoecology (Sander and Gee, 1990). At Star Carr, a Mesolithic settlement site of major importance in Yorkshire (Mellars and Dark, 1998), detailed studies of charred macroscopic plant remains have indicated that seasonal reedswamp burning took place (Hather, 1998; Law, 1998).

Despite the limitations outlined above, microscopic and macroscopic charcoal analyses are useful tools for interpretation of fire history, providing evidence for different types of fire events. Therefore, both microscopic and macroscopic charcoal were analysed to obtain information relating to both regional and local fire events.

Laboratory methods

a) Microscopic charcoal

The most convenient and therefore usual practice for microscopic charcoal has been to prepare and count it with pollen, so to allow discussion in the context of existing work this approach was maintained here. Charcoal particles break down during pollen preparation and the degree of

distortion of potentially useful information relating to size class appears to vary with the preparation techniques used (Tinner and Hu, 2002). Hence, Clark's (1982) point count method was used to estimate the area of microscopic charcoal per cubic centimetre of sediment. A magnification of 200 x was selected so that most charcoal particles only came into contact with one point on an eyepiece micrometer to minimise count distortion by non-random occurrence of larger particles (Tolonen, 1986). For each field of view, the number of micrometer points that were in contact with charcoal and the number of *Lycopodium* spores touching the micrometer were counted. This was repeated for one hundred random fields of view per sample, comprising ten fields of view across each of ten regularly spaced parallel traverses. The following formula was then used to estimate charcoal area per unit volume of sediment:

$$\text{Charcoal area} = (CA/N) \times (L_1/VL_2)$$

where C is the number of points falling on charcoal, A is the area of field of view (cm^2), N is the total number of micrometer points, L_1 is the total number of *Lycopodium* spores added, V is the volume of sediment used (cm^3) and L_2 is the number of *Lycopodium* spores observed.

b) Macroscopic charcoal

For macroscopic charcoal, samples were collected from the same core depths used for pollen. Non-contiguous sampling was considered satisfactory for providing a general indication of change, and although it meant some fire events would be missed, it allowed more time for other analyses. One cubic centimetre of peat was gently washed and wet-sieved to obtain the 150 μm to 250 μm size class, which was selected for analysis as it has been found to be the most practical size range for this type of study (Whitlock and Larsen, 2001). Charcoal particles were distinguished from other dark organic matter by their black, opaque, angular appearance, iridescent sheen under artificial light and appearance upon crushing with a dissecting needle (Whitlock and Larsen, 2001). The number of particles was counted for the entire sample retained on the 150 μm sieve at 40 x magnification under a stereomicroscope to give particles per cm^3.

Data analysis and interpretation

a) Microscopic charcoal

For microscopic charcoal, the charcoal area obtained from Clark's (1982) point count method was then divided by the pollen concentration for the sample to give the charcoal to pollen ratio (C:P index), as cm^2 per pollen grain. The C:P index was developed by Swain (1973) as an aid to detecting 'real' fires, as it is not sensitive to the effects of altered rates of sedimentation. It was also designed to take account of a presumed reduction in pollen accumulation following vegetation loss from burning, which would maximise the value of the C:P index for a given quantity of charcoal (Tolonen, 1986; Whitlock and Larsen 2001).

b) Macroscopic charcoal

For macroscopic charcoal, any sample where the particle count exceeded 50 cm^{-3} was taken to have experienced a local fire event (Whitlock and Larsen, 2001). For all core sites, counts were plotted on the pollen diagram alongside the C:P index. Microscopic and macroscopic charcoal records were analysed together in an attempt to make inferences about fire activity in the palaeoecological record.

Summary

This chapter has explained the approach that will be taken to investigating long-term vegetation dynamics and reconstructing past vegetation for Caledonian pine forest. The surface sampling methods discussed will be used to improve understanding of the pollen-vegetation relationship in the study area, and to validate the Prentice model of pollen dispersal (Prentice, 1985) before later using it as a tool in the landscape reconstruction process.

Plausible reconstructions need also to be based on ideas about vegetation change inferred from palaeoecological records, so cores were taken from a range of basin types and sizes to collect evidence for vegetation change at different scales. Major zones were identified and age estimates for their boundaries derived from tephra horizons and previously published dates for key events. Pollen, stomata and charcoal data were interpreted from pollen diagrams in terms of local and regional vegetational zones, and local basin vegetation was inferred from peat stratigraphy,

stomata and pollen. Inferences about human activity were made from changes in the charcoal record and where possible, from the occurrence of rare taxa.

The following chapters present the results obtained by application of these methods. In chapter 3, the spatial properties of the pollen signal are explored using modern pollen and stomata data. In chapter 4, the development of theoretical pollen analysis is reviewed and the usefulness of the Prentice (1985) model for Caledonian pine forest landscapes is assessed. Chapters 5 and 6 present palaeoecological records for two regional and five local sequences, which are interpreted using traditional pollen analysis techniques. In chapter 7, the inferences about vegetation change from these profiles, together with those from previous studies of the area, are used to advance hypotheses derived for landscape creation and testing using pollen dispersal modelling. The best fit landscapes are then used to suggest plausible past landscapes for the study area. Finally, in chapter 8, the contribution the approaches taken can make to nature conservation is discussed, and the extent to which the original aims of the thesis have been realised is critically assessed.

Chapter 3. Inferring community composition and vegetation openness in Caledonian pine forest from surface samples of pollen and *Pinus* stomata

Introduction

This chapter aims to investigate the modern pollen-vegetation relationship in Caledonian pine forest, focusing on its spatial sensitivity in relation to detecting forest openness and its usefulness for identifying plant communities from their pollen signals. From this, the value of the modern pollen signal as an aid to interpreting fossil assemblages will be assessed. The usefulness of *Pinus* stomata as a tool for indicating the local presence of *Pinus* will also be explored.

Pollen-vegetation relationships

If palaeoecological records are to be useful for reconstructing past environments or landscapes, the information they contain needs to be interpreted in terms of past biotic and abiotic components of the ecosystem (Birks and Birks, 1980). Interpretation of palaeoecological records is based on two major assumptions: that the relationship between the signal (*e.g.* pollen or macrofossils) and the environment (*e.g.* the surrounding vegetation) is consistent in space and time, and that it is possible to understand its complexity. In pollen analysis, it has long been recognised that there is a quantitative relationship between the number of pollen grains of a taxon deposited at a site and the number of individuals of that taxon in the surrounding vegetation (von Post, 1916 in von Post, 1967; Davis, 1963; Andersen, 1970; Birks and Gordon, 1985). If these assumptions are true, studying the modern pollen-vegetation relationship should be a useful aid to interpreting past pollen data in terms of past vegetation.

Various approaches have been designed to achieve this, including analogue matching, the use of indicator species (reviewed by Birks and Birks, 1980) and modelling (reviewed by Jackson, 1994; see also chapter 4). All these methods have associated problems for reconstruction of past vegetation. Analogue matching involves extrapolation of the present into the past (Birks and Birks, 1980), and is a common approach within all branches of natural science (Overpeck *et al.*, 1985). One method widely used with pollen data is the modern analogue technique, which was outlined in chapter 2. A limitation of this approach is that it requires a large and varied modern

spectra dataset collected from a wide range of vegetation types and geographical locations with which to statistically compare the fossil spectra, and this may not always be available (Fall, 1994). Also, erroneous matches may occur or acceptable modern analogues missed due to errors introduced when selecting dissimilarity cut-off values at the comparison stage (Wahl, 2004). There are also difficulties associated with the interpretation of fossil pollen spectra from 'non analogue communities' (Overpeck *et al.*, 1985; Delcourt and Delcourt, 1991; Williams *et al.*, 2001; Birks, 2003).

The indicator species approach also relies on analogue matching but uses known associations and ecological tolerances of plant taxa to make inferences about the past environment (Birks, 1983). It assumes that these relationships and preferences have not changed over time but this does not take account of likely changes in competitive conditions as plant communities evolved (Birks and Birks, 1980). The modelling approach to landscape reconstruction is discussed in detail in chapter 4, but this also has limitations. Although simplified models of pollen dispersal and deposition have been used to generate valid predictions for a variety of site and vegetation combinations (*e.g.* Sugita, 1994; Sugita *et al.*, 1999; Nielsen, 2004), models require calibration and validation before they can be applied to landscape reconstruction. Calibration is necessary as many of the input parameters are estimates (*e.g.* pollen fall speed and relative pollen productivity) and methods for collection of pollen and vegetation data still need to be standardised and further refined. Validation is ongoing and involves testing the models using empirical vegetation data and comparing the simulated pollen with empirical pollen records (*e.g* Sugita, 1994; Broström *et al.*, 1998; Nielsen, 2004).

Usefulness of stomata

Non-pollen indicators can also be a useful complement to pollen analysis for reconstructing past vegetation. The main ones used so far are plant macrofossils and conifer stomata, both of which are usually interpreted as indicators of local plant presence. This is useful because pollen alone may be misleading in some circumstances, such as in tree line studies where non-local tree pollen may mask local production (Birks and Birks, 2000). Also, it is probably not possible to use pollen alone to distinguish between small patches of locally present vegetation and large patches of regionally present vegetation (Jacobson and Bradshaw, 1981). There is evidence that, in combination with the additional information from stomata and macrofossils, improved interpretations of fossil records may be made (Birks and Birks, 2000). The potential value of

stomata as indicators of past *Pinus* presence can be assessed by exploring presence or abundance of stomata in relation to distance from *Pinus* trees (see chapter 2).

Spatial sensitivity of pollen signal

All inferences about vegetation made from fossil pollen data are based on assumptions about pollen source area, which is the area from which most of the pollen from a taxon is derived (Jackson, 1994). An understanding of pollen source area is therefore important for estimating the spatial scale at which the pollen signal is recording the landscape (Sugita, 1994; Sugita *et al.*, 1999). This is not straightforward, as different taxa are reflected in the pollen signal in different ways, *e.g.* tree pollen tends to be abundantly produced and widely dispersed (Prentice, 1986), whilst that of small shrubs and herbs tends to be reflected at small scales of a few metres, (*e.g.* Evans and Moore, 1985; Pardoe, 1996; Hjelle, 1998; Bunting, 2003), because the pollen is released closer to the ground (Faegri and Iverson, 1989).

Pollen source area has been conceptualised in several different ways (see chapter 4). For openings in closed forest landscapes, Jacobson and Bradshaw's (1981) model predicts that pollen source area will vary between taxa depending on the size and type of site as well as the properties of the pollen type itself. Empirical evidence supports the prediction that smaller, heavier pollen types will have smaller source areas, and larger basins will have larger source areas (Jacobson and Bradshaw, 1981; Bradshaw and Webb, 1985). In patchy landscapes such as Caledonian pine forest, the pollen-vegetation relationship is more complex, as it is more difficult to separate the local pollen signal from the 'background' pollen signal due to the same taxa being common to both (Sugita, 1994).

An alternative concept of pollen source area is defined for such landscapes, the 'relevant source area of pollen' (RSAP), proposed by Sugita (1994). This is defined as the distance from the sampling point beyond which the correlation between distance-weighted plant abundance and pollen loading (*i.e.* average pollen deposition per unit area; Davis, 2000) does not improve. Plant abundance is distance-weighted to take account of the greater effect on the pollen signal of plants closest to the sampling point (Prentice, 1985; Sugita, 1993, 1994). The RSAP will vary according to the characteristics of the plants (*e.g.* pollen dispersal mechanism, size and shape of pollen grain) and the size and type of basin sampled (Bunting, 2003). As *Pinus* is the dominant tree taxon in Caledonian pine forest today, obtaining an estimate of RSAP for *Pinus* should give

some indication of the scale at which present day landscape openness is recorded by the pollen signal.

A potential problem associated with the interpretation of past pollen signals is that pollen source area is likely to have changed if the size of the opening changed or if the local component of the signal (*i.e.* that derived from shrubs and herbs growing on the bog surface) changed as a result of basin succession, fire or other processes. The effect of size can be explored empirically by comparing the pollen signals for different sized basins with similar vegetation, and although the effects of basin succession cannot be assessed directly, pollen assemblages from similarly sized basins representing a range of community types (*e.g.* fen, bog and dry heath) can be used to explore the variability of the pollen signal for different basin types.

Landscape openness has also been estimated from pollen signals by comparing the percentage of arboreal pollen (AP) to non-arboreal pollen (NAP) in the pollen assemblage. Estimates of the percentage of *Pinus* indicative of local *Pinus* presence vary slightly: Bennett (1984) suggests >20% AP whereas Clayden *et al.* (1985) suggest >15%. Vera (2000) suggests that <= 10% NAP is indicative of closed forest. However, recent modelling suggests that the relationship between NAP and openness is not straightforward. Sugita *et al.*(1999) point out that NAP percentage has often been uncritically used to infer past landscape openness and suggest it should be regarded as qualitative or semi-quantitative, as no correction factors or calibration functions are used (Sugita *et al.*, 1999). Conversely, Svenning (2002) reviews evidence from *c.* 20 studies involving NAP percentages and other openness proxies such as beetles, molluscs and plant macrofossils and suggests that percentage NAP can provide a fairly robust indication of openness.

Caledonian pine forest is particularly suitable for investigating the spatial properties of the pollen-vegetation relationship as it is a relatively simple ecosystem. The insights obtained should contribute to improved interpretation of palaeoecological data, and hence, a better understanding of how long-term vegetation dynamics is recorded in the pollen signal, which in turn should lead to improved landscape reconstructions.

Error analysis

In chapter 2, the importance of identifying the main sources of error in pollen analysis was discussed. Lack of replication of palaeoecological records below the regional scale has made estimation of the inherent variability of the pollen signal difficult, whilst other sources of error relate to count size (Maher, 1972; Birks, 1993). For this study, it is important that the count size selected is sufficient to enable the distinction of major vegetation units and openness in Caledonian pine forest, whilst avoiding unnecessary effort that could usefully be directed at analysis of more samples. The optimum count size required to achieve this can be investigated using surface sample studies.

Aims

For Caledonian pine forest, the once extensive natural forest is much reduced and modified, but analysis of the modern pollen-vegetation relationship should provide some useful information to aid the interpretation of present day communities. In this chapter, the aims are to use surface samples to i) study how the modern pollen signal reflects communities present today; ii) assess usefulness of *Pinus* stomata in detecting local presence of *Pinus*; iii) explore the pollen signal in relation to *Pinus* canopy openness; iv) identify the minimum effort required to achieve the desired level of confidence in the data.

Study area

The importance of Caledonian forest and its development since the early Holocene is discussed in detail in chapter 1. A description of the Abernethy nature reserve and a map of the 15 km x 15 km study area (Fig. 1.1) are also given in chapter 1. The present day landscape in Abernethy Forest comprises a range of environments, in terms of both the plant communities present and their distribution within the landscape. The northern part of the reserve is characterised by a mosaic of *Pinus* forest interspersed with numerous bogs. The field layer predominantly comprises *Calluna, Vaccinium* spp., mosses and on occasion, grass species (RSPB, 2002). Further south, there is extensive open heath with scattered *Pinus*, open blanket bog and small amounts of juniper scrub and birch woodland. Several pockets of mixed forest occur. The range of communities common to Caledonian pine forest are well represented, which makes Abernethy Forest particularly suitable for this type of study.

Table 3.1. Sites sampled for pollen from defined communities. All sites were 100 x 100m except L8 and L12 (50 m x 50 m).

Site No.	Location	National Grid Reference (NW corner)	Community description	NVC category
L1	NE of Loch Garten	29813 81861	Bog with scattered pine	M18 *Erica-tetralix-Spahagnum papillosum* mire
L2	N of Loch Garten	29776 81860	Pine/birch woodland	W18 *Pinus* sylvestris-*Hylocomium splendens* woodland
L3	Memorial Wood	30098 81338	Pinewood with *Vaccinium*	W18 *Pinus* sylvestris-*Hylocomium splendens* woodland
L4	Rynettin	30154 81469	Birch woodland with *Calluna*, *Vaccinium* and poor flushes	W4 *Betula pubescens-Molinia caerulea* woodland
L5	Tulloch Moor	29631 81642	Dry *Calluna* heath	H12 *Calluna vulgaris-Vaccinium myrtillus* heath
L6	W of Duack Burn, Tore Hill	29931 81840	Bog with scattered pine	M18 *Erica-tetralix-Spahagnum papillosum* mire
L7	North Abernethy	30010 81855	Pinewood with *Calluna*	W18 *Pinus* sylvestris-*Hylocomium splendens* woodland
L8	E of River Nethy	20228 81376	*Juniper* thicket	W19 *Juniperus communis-Oxalis acetosella* woodland
L9	Carn a'Chnuic	30419 81451	Pinewood with Poaceae (grass)	W18 *Pinus* sylvestris-*Hylocomium splendens* woodland
L10	W of Duack Burn, Tore Hill	29950 81790	Bog with scattered pine	M18 *Erica-tetralix-Spahagnum papillosum* mire
L11	South of Allt Bheadhair, south Abernethy	30327 81178	Blanket bog	M19 *Calluna vulgaris-Eriophorum vaginatum* blanket mire
L12	E of Faesheallach Burn, SE of Loch a'Chnuic	20560 81396	Sedge mire in open blanket bog area	M6 *Carex echinata-Sphagnum fallax/denticulatum* mire

Methods

Full details of methods used for surface sampling from moss polsters are given in chapter 2. Where possible, *Sphagnum* spp. were sampled, collecting around 20 cm^3 of the green parts of the moss. A set of samples for community identification was collected (set L, $n = 119$) and a second set for the openness study (set SST, n = 29); for locations see Chapter 2, Fig. 2.1. Standard methods for preparation and counting of pollen and stomata from surface samples (*e.g.* Moore *et al.*, 1991) were used for all samples. Pollen was counted to *c.* 300 grains Total Land Pollen (TLP). Full details are given in chapter 2. Data from the RSPB W18 woodland field layer mapping project (RSPB, 2002) and National Vegetation Classification (NVC) data from Abernethy Forest were initially used to locate potential areas for surface sampling, and from these a range of typical communities and a representative openness gradient were identified.

i) Community characterisation

For interpretation of the palaeoecological record in Caledonian pine forest, it would be useful to know the extent to which major communities such as fen, bog, dry heath, *Pinus* forest and *Betula* woodland can be identified by their pollen signals and whether there is any difference in the signal between *Pinus* canopies with different taxa dominating the field layer, *e.g. Vaccinium*, *Calluna* or Poaceae. Samples from under the canopy would be expected to reflect the surrounding vegetation at a small scale similar to that of forest hollows (Calcote, 1995), whilst those from open areas would be expected to have much greater pollen source areas (Jacobson and Bradshaw, 1981; Sugita, 1994). The small scale spectra were intended to be used to aid the interpretation of fossil assemblages where canopy closure was inferred (*e.g.* by the presence of wood macrofossils, pine needles or stomata). Multiple samples were prepared from each community to explore the local variability of the pollen signal and identify the extent to which the signals were distinctive for each community type.

In March 2003, a set of moss samples (set L, $n = 119$) was collected from 12 locations (for 11, $n = 10$; for 1, $n = 9$; for location map see chapter 2, Fig. 2.1). Areas with relatively homogeneous vegetation cover were selected from a range of typical community types throughout the reserve as shown in Table 3.1. Depending on the size of the patch, the areas from within which samples were taken were 50 m x 50 m or 100 m x 100 m, in each case ensuring there was a buffer of similar vegetation for at least a further 10 m around the sampling area to minimise the effect of local pollen from a different community on the signal. All sampling sites were geo-referenced

using a handheld Garmin GPS and approximate distances from the sampling point to the nearest *Pinus* (individuals and woodland) and other adjacent vegetation were measured.

Data analysis

For all 119 samples, only the major taxa (*i.e.* all those that occurred at >5% TLP in at least one sample) were used for further analysis, with pollen proportions re-calculated from a pollen sum of these taxa only. The structure of the data was analysed numerically using two-way indicator species analysis (TWINSPAN) (Hill, 1979; Oksanen and Minchin, 1997) and Ward's hierarchical cluster analysis to identify the extent to which community signals could be grouped on the basis of pollen assemblage alone.

TWINSPAN (Hill, 1979; Oksanen and Minchin, 1997) was performed on square root transformed pollen proportional data for major taxa (those occurring at >5% TLP in one or more samples). TWINSPAN performs a hierarchical classification based on successive division, based on ordination by correspondence analysis. Pseudospecies are created to represent different levels of abundance, for which the cut levels were set at 0, 2, 5, 10, 20 and 40%.

For the main taxa (>5% TLP, as above), cluster analysis was performed for square root transformed proportional data. The purpose of this was to explore the similarities between the samples with no *a priori* assumptions made on the basis of location, *i.e.* using only the pollen percentages. The analysis was performed using the program CONISS (Constrained Incremental Sum of Squares; Grimm, 1987), using the unconstrained option. This is suitable for samples that have no stratigraphic relationship, and allows all samples to cluster freely. A pollen diagram based on the main clusters was constructed for each method and the extent to which the resultant sample groupings reflected the site-based vegetation community data was explored. The original pollen and vegetation data were used to identify possible sources of discrepancy or anomalous samples. The mean pollen percentages for major taxa (>5% TLP) for samples in the strongest cluster analysis and TWINSPAN groups were then compared with the mean pollen percentages of each vegetation type.

ii) Assessing usefulness of Pinus *stomata*

The number of *Pinus* stomata on the pollen slides was counted at the same time as pollen. For surface sample set L, the presence of local trees was expressed in terms of the distance to the

nearest individual tree or stand of *Pinus* as measured from the centre of each 100 m x 100 m plot (50 m x 50 m for L6). Where scattered *Pinus* occurred within the plot, the mean distance of the four nearest trees was taken. A value of zero indicates that samples were taken beneath a *Pinus* canopy.

iii) Sensing canopy openness from basin mires

It would be useful to be able to interpret palaeoecological records in terms of simple categories of forest openness (*i.e.* closed forest, semi-open or open). In this study, openness is defined using percentage *Pinus* cover, as *Pinus* is the dominant canopy forming tree in the present day forest. The more open the landscape, the more likely it is that pollen source areas will be large, as the basins in open landscapes are more likely to be surrounded by open areas as well as forested areas. It was intended that the palaeoecological records for this study be collected from basins measuring between *c.* 60 m and 100 m diameter to obtain records reflecting the landscape at a small to medium scale, so surface samples were collected from a range of approximately circular opening sizes within this range to investigate the extent to which openness could be detected for sites from this size range. Pollen assemblages from different sized basins were compared with surrounding *Pinus* cover to explore how different sized openings reflect openness. The effects of basin size on pollen source area are explored further using modelling in chapter 4.

Site selection.

A set of moss samples (set SST, $n = 29$) were collected along an openness gradient from closed forest to semi-open forest to open bog to be used for detecting openness and estimating the spatial resolution of the pollen signal (Fig. 2.1). In the closed and semi-open forest, samples were collected from the approximate centre of canopy openings 60 m to 100 m diameter to minimise the local pollen component of the pollen signal (Jacobson and Bradshaw, 1981; Calcote, 1995). Several samples were also collected from open bog (> 100 m diameter or < = 1 km from *Pinus*).

Openness categories

Five openness categories were defined based on percentage *Pinus* cover in the area around each sample point within a radius of 500 m as shown in Table 3.2. Percentage *Pinus* cover was calculated from RSPB (2002) field survey data which was first prepared using ESRI ArcMap v 9.0 for use with PolFlow (Bunting and Middleton 2005). PolFlow is designed chiefly for pollen

dispersal modelling (see chapter 4) but in this case was used to calculate *Pinus* abundance data within the specified radius. All 29 samples were then allocated to the appropriate openness category (Table 3.2) and a one-way analysis of variance (ANOVA) performed on the *Pinus* percentage data.

Data analysis:

To give an approximation of the spatial sensitivity at which these sites reflect *Pinus* pollen, area of *Pinus* cover (m^2) was calculated for each of a series of concentric rings (20 m width to 100 m then 100 m width to 2000 m) around each sampling point for i) small openings (< 60 m diameter), ii) medium openings (60-100m diameter) and iii) open areas (> 100 m diameter). *Pinus* abundance to the nearest 10 m x 10 m was obtained from the RSPB (2002) field layer survey. Distance weighting in the form of 1/d and $1/d^2$ was calculated and the Pearson correlation coefficient calculated for percentage *Pinus* pollen and cumulative *Pinus* abundance at each incremental distance.

Table 3.2. Openness categories used for classification of set SST surface samples. Percentage cover was estimated for the area within a radius of 500 m around each pollen sampling point.

Openness category	Description	Percentage *Pinus* cover within 500 m radius
1	Open	0
2	Mainly open	<20
3	Semi-open	20-50
4	Mainly closed	>50-70
5	closed	>70

iv) Minimisation of effort

In order to establish the degree to which vegetation types and openness categories can be distinguished at lower counts than are traditionally used in pollen analysis, 95% confidence intervals were calculated for all pollen samples (Mosimann, 1965; Maher, 1972, 1981). This is a measure of the probability of being able to reproduce the count from another pollen slide of the same sample (Birks and Birks, 1980) and is a function of the percentage of the taxon present and the size of the count. It allows evaluation of the precision of the percentages displayed on the pollen diagram (Maher, 1972).

95% confidence intervals (Maher, 1972, 1981) were calculated in Excel for major taxa (those occurring at levels > 5%) for all the set L surface samples and the results compared for all the site, TWINSPAN and cluster analysis groups. These were also displayed on a pollen diagram, which were calculated in *psimpoll* v. 4.10 (Bennett, 2002) using the same method. This enabled identification of clusters where a higher pollen count is necessary to distinguish between community types. For comparison of the L set clusters, TWINSPAN and site-based groups, 95% confidence limits were also applied for each group mean, using standard methods to propagate the counting error when deriving the standard error of the mean (Parratt, 1961). The effect of count size on cluster differentiation was also explored by applying confidence limits to the percentage data at a lower pollen sum of 150 TLP.

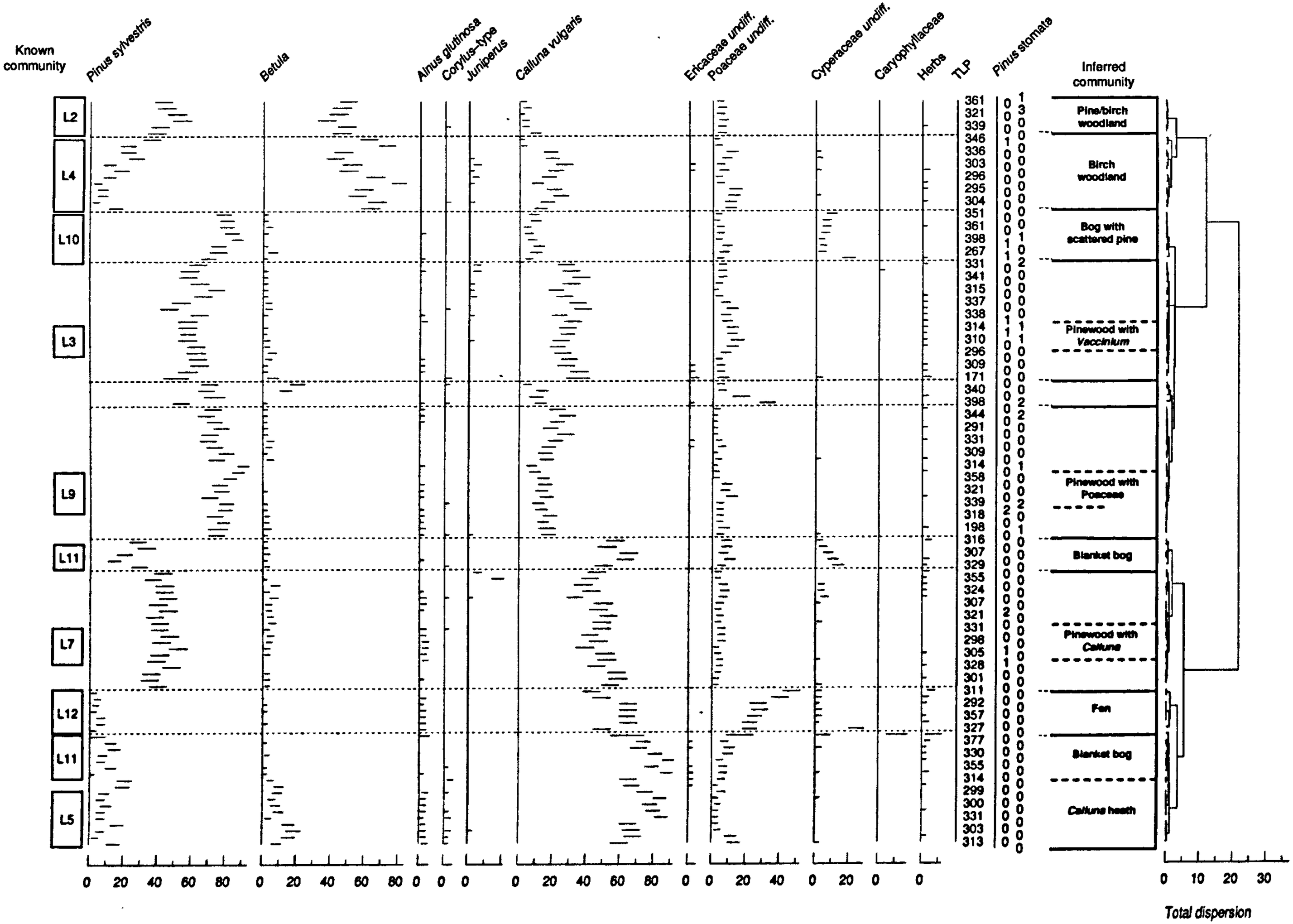
Results

i) Community characterisation

Fig. 3.1 shows the surface sample percentage pollen data ordered by cluster analysis group. *Pinus* stomata counts are also shown. Visual inspection shows that the main groups are formed on the basis of variations in just five taxa (*Pinus*, *Betula*, *Calluna*, Poaceae and Cyperaceae). In both the cluster and TWINSPAN analyses, four community types (mixed woodland, *Betula* woodland, *Calluna* heath and fen) showed distinctive pollen assemblages on the basis of these five taxa (Fig. 3.2). These formed separate groups with both cluster analysis and TWINSPAN, and only one group, open heath (Fig. 3.2c) contained any samples from a different community. The mean pollen proportions for known community type, cluster and TWINSPAN groups are shown in Fig.3.2. Of the three sites selected from bogs with scattered *Pinus*, only samples from site L10 form distinct groups on the basis of <15% *Calluna* pollen and >5% Cyperaceae pollen (cluster analysis, n = 8; TWINSPAN, n = 6). Open bog (L11) can be distinguished from all other communities except fen (also taken from an open context) on the basis of low *Pinus* pollen (<20%) but formed two clusters on the basis of variable Cyperaceae: one with <0.3% and a second group with > 3% Cyperaceae pollen.

Fig.3.1. (overleaf). Percentage pollen diagram showing Maher's (1981) confidence intervals and groups defined by Ward's cluster analysis. Clustering of five or more samples from the same known community (L) is shown in the boxes on the left; spaces represent clustering with no meaningful relationship to known community type. Community types are shown next to the dendrogram; those shown within dotted lines cannot be distinguished from other similar communities on the basis of the assemblages used here.

Abernethy Forest surface samples



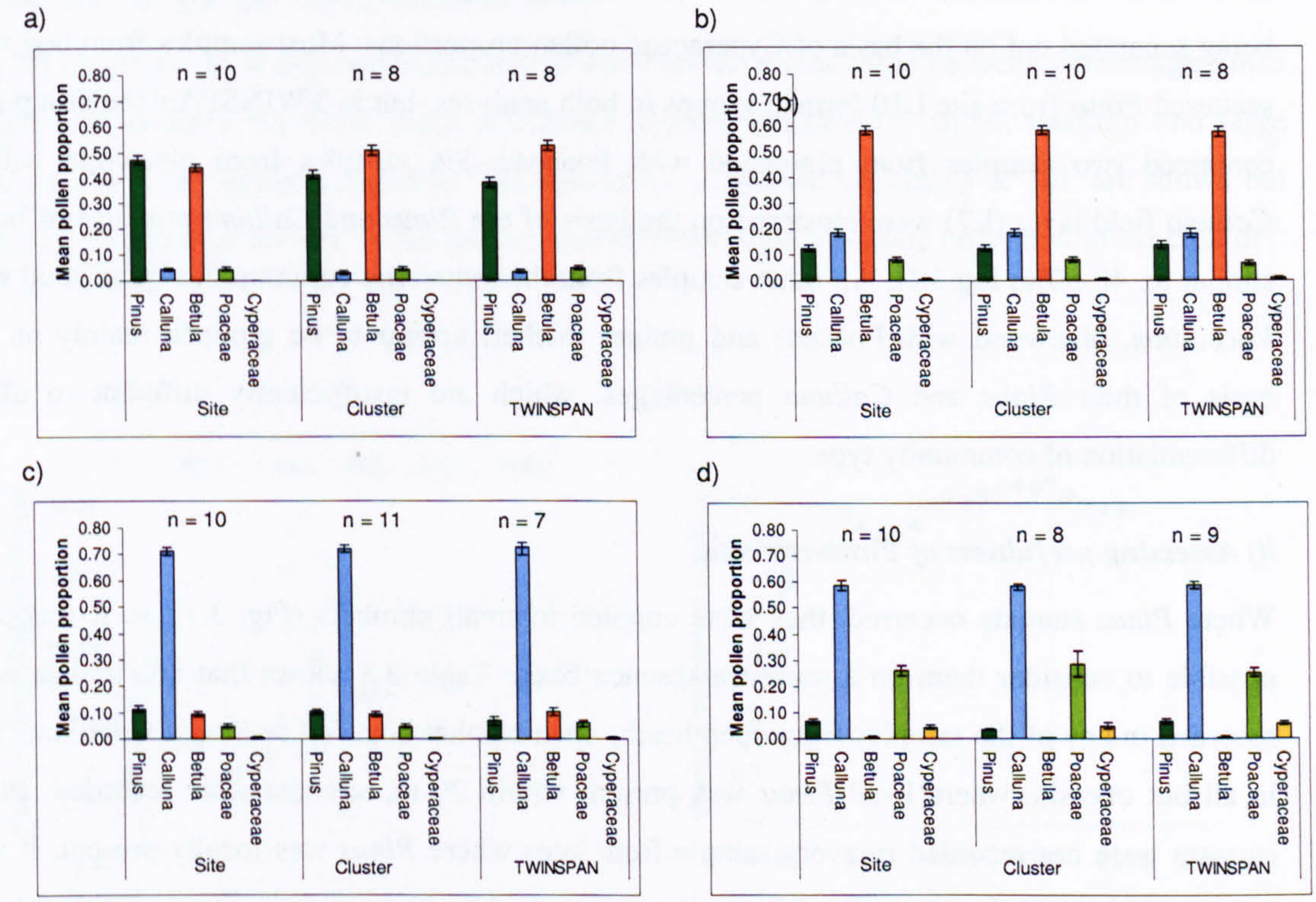


Fig. 3.2. Selected comparisons of cluster analysis and TWINSPAN groups with known community type, showing mean pollen proportions for each group based on five major taxa. a) mixed woodland; b) *Betula* woodland; c) open *Calluna* heath; d) fen; e) forest bog with scattered *Pinus* (>5% Cyperaceae). Error bars show standard error of the mean and incorporate counting error calculated using Maher's (1972) method.

In TWINSPAN, samples were grouped with fen and bog with scattered *Pinus* in addition to being separated out on the basis of Cyperaceae pollen proportions. Most samples from bog with scattered *Pinus* from site L10 formed groups in both analyses, but in TWINSPAN the group also contained two samples from pinewood with Poaceae. Six samples from pinewood with a *Calluna* field layer (L7) were clustered on the basis of the *Pinus* and *Calluna* proportions being similar (*c.* 40-50%; Fig.3.1). All other samples from the remaining communities (pinewood with *Vaccinium*, pinewood with Poaceae and juniper thicket) appear to be grouped mainly on the basis of their *Pinus* and *Calluna* percentages, which are insufficiently different to allow differentiation of community type.

ii) Assessing usefulness of Pinus *stomata*

Where *Pinus* stomata occurred, they were counted in small numbers (Fig. 3.1), so it was only possible to consider them on a presence/absence basis. Table 3.3 shows that no stomata were recorded in any of the samples from open heath, open blanket bog, fen or *Betula* woodland, and in all but one site where local *Pinus* was present within 20 m, stomata were recorded. *Pinus* stomata were not recorded in every sample from sites where *Pinus* was locally present. It was not possible to use the presence of *Pinus* stomata to further separate any community signals, as those which were indistinct all occurred in communities where *Pinus* was locally present. Only two of the 29 SST samples contained *Pinus* stomata.

Table 3.3. Total *Pinus* stomata recorded for $n = 10$ (L12: $n = 9$) samples from 12 sites in the Abernethy Reserve. Nearest *Pinus* is calculated from the mean of the distance to the nearest tree or stand of trees from the centre of each 100 m x 100 m study area (50 m x 50 m for L6). For sites with scattered *Pinus* (L1, L6, L10), the mean distance to the nearest four trees was used. A value of zero metres indicates that samples were taken beneath the *Pinus* canopy.

Site	Vegetation type	Nearest *Pinus* (m)	Total *Pinus* stomata
L1	Bog with scattered pine	10	0
L2	Pine/birch woodland	0	4
L3	Pine woodland	0	3
L4	Birch woodland	150	0
L5	Dry heath	100	0
L6	Bog with scattered pine	10	2
L7	Pine woodland	0	5
L8	Juniper thicket	20	2
L9	Pine woodland	0	8
L10	Bog with scattered Pinus	10	3
L11	Open blanket bog	500	0
L12	Sedge mire	200	0

ii) Sensing canopy openness from basin mires

Fig 3.3 shows plots of the correlation coefficient r for the relationship between percentage *Pinus* pollen and distance weighted plant abundance against distance for small, medium and large openings, and all openings together. The results for a distance weighting of $1/d^2$ are shown but 1/d produced similar results. It can be seen that the relationship is quite noisy and in the case of

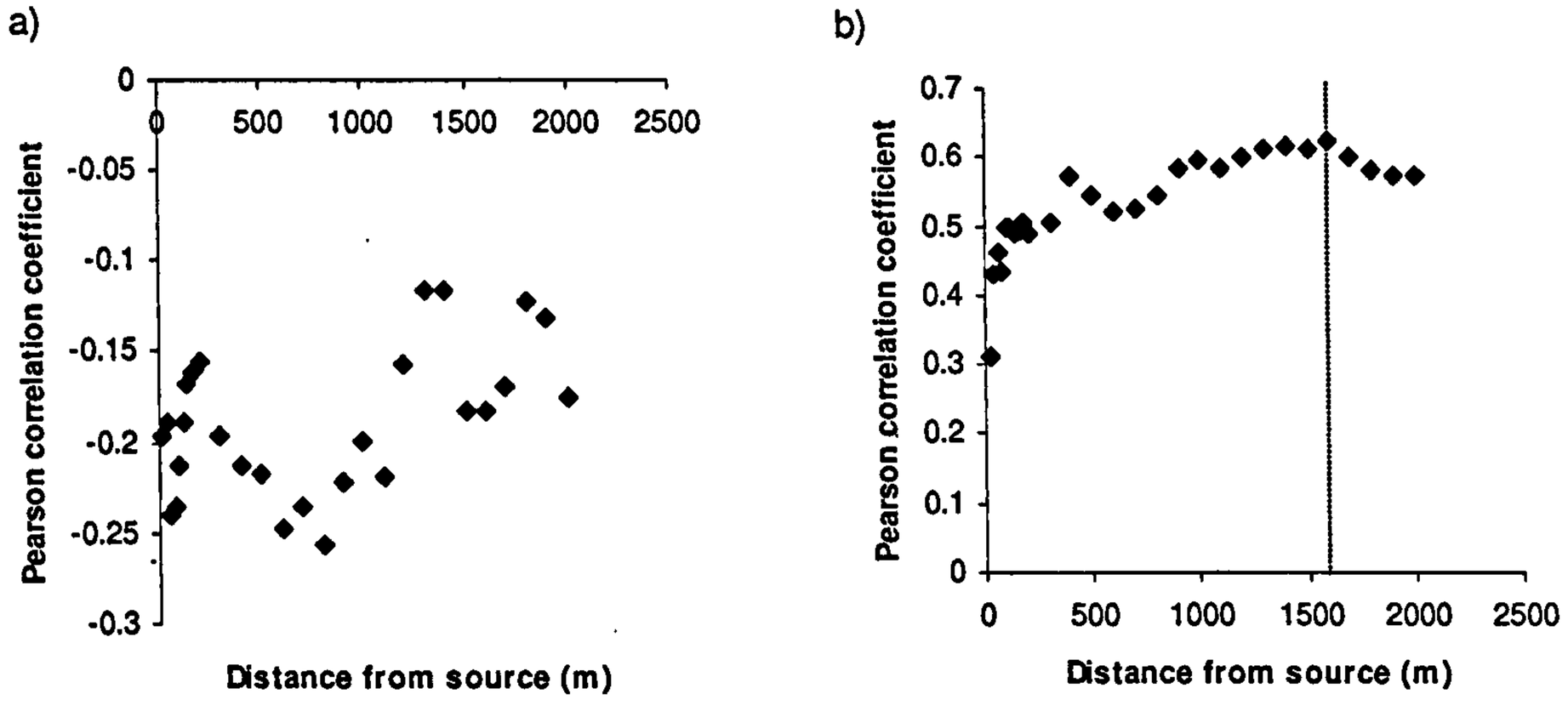


Fig.3.3. Plots of Pearson correlation coefficient for the relationship between percentage *Pinus* pollen and distance-weighted *Pinus* abundance against distance from sample point for a) small openings (< 60 m diameter; n = 13); b) medium openings (60-100 m diameter; n = 6); c) large openings or open areas (>100 m diameter; n = 7); d) all samples. The distance at which the correlation does not improve is most apparent in d), where RSAP is therefore estimated at 800m. The distance weighting used was $1/d^2$.

small (< 60 m diameter) basins the correlation between percentage *Pinus* pollen and surrounding *Pinus* is negative. For medium sized basins (60 m -100 m, Fig. 3.3b), the correlation does not improve beyond *c.* 800 m, so this is the estimated RSAP. RSAP could not be reliably estimated for large openings (Fig. 3.3c) due to the level of noise. If all sites are analysed together, a clear asymptote is apparent, also at *c.* 800 m; a peak in the values of the correlation coefficient between 1250 and 1500 m is likely to be related to a variation in the spatial pattern of the vegetation detectable in a consistent way by the sites used .

The results of the ANOVA (Table 3.4) show that there is a significant difference in the mean *Pinus* pollen percentages for four openness categories. No samples fell into the mainly closed category. A *post-hoc* Tukey HSD test (Table 3.5) was used to establish which means were significantly different from the others. This showed that the *Pinus* percentages from the open sites were significantly different from mainly open, semi-open and closed sites, but no other differences were significant. Mean *Pinus* pollen percentage for open sites was 8%, for partly open sites 67%, for semi-open sites 54% and for closed sites 72%.

Table 3.4. One-way analysis of variance for percentage *Pinus* pollen in four openness classes.

	Sum of squares	df	Mean square	*F*	*P*
Between groups	11037.7	3	3679.3	6.79	0.002
Within groups	13556.9	25	542.3		
Total	24594.7	28			

Table 3.5. Post-hoc Tukey HSD test from results of one-way ANOVA on percentage *Pinus* pollen for four openness classes. The bottom left triangle of the array shows the Studentized range statistic Q and the upper right triangle of the array (italics) the probability, *p*

	open	mainly open	semi-open	closed
open		*0.002196*	*0.01798*	*0.001117*
mainly open	5.785		*0.814*	*0.991*
semi-open	4.537	1.248		*0.6469*
closed	6.201	0.4161	1.664	

iv) Minimisation of effort

The most robust community signals were identified as those where there was no overlap in the range of pollen percentages indicated by the confidence intervals and where the TWINSPAN and cluster analysis groups most closely resembled the known vegetation groups. As the communities that could be distinguished from each other were quite different (in particular, the relative proportions of *Pinus*, *Betula*, *Calluna* and Poaceae) it was considered likely that this level of differentiation could be achieved using a lower count size. Confidence intervals were recalculated for the percentage data using an arbitrary count size of 150 TLP to observe the effect this would have on cluster distinction. Although the error bars spanned as much as 15% for some samples (compared with as much as 10% for a 300 count size), there was still no overlap in the signals, *i.e.* the same level of differentiation was possible as achieved with higher counts of *c.* 300 TLP.

Discussion

i) Community identification

The community signals studied suggest that open communities (fen, blanket bog and heath) and woodland with birch locally present can be readily distinguished from all categories of *Pinus* woodland even at counts of *c.* 300 grains TLP. The 95% confidence intervals (Fig. 3.1) show that there is no overlap in the percentages of *Pinus* and *Betula* pollen with those of other communities. The association of *Pinus* values below 20% with an absence of trees within 100m, as seen in sites L4 and L11, supports Bennett's (1984) suggestion that >20% *Pinus* pollen is required to infer local presence of *Pinus*. It may be possible to identify pinewood communities with *Calluna* from those with *Vaccinium* or Poaceae field layers when sampling under the canopy, but a greater range of sites is required to establish this. It may be possible to further differentiate between *Pinus* dominated communities on the basis of an NAP pollen sum, and there is scope for using macrofossils to identify local presence of taxa under-represented in the pollen record such as *Vaccinium*.

Cyperaceae may be too locally variable for it to be a useful indicator of vegetation type, which supports the findings of Overpeck *et al.* (1985). Similarly, *Juniperus* was locally variable, possibly a reflection of its dioecious nature. Given also its poor survival in the pollen record, it

was not considered a particularly useful taxon for differentiating plant communities on the basis of pollen signals, hence its exclusion from the TWINSPAN and cluster analyses.

ii) Assessing usefulness of Pinus *stomata*

Quantitative analysis of the stomata was not considered appropriate for the small counts present in these samples, but they could be considered on a simple presence/absence basis. Although absence cannot be taken as indicative of absence of trees, presence was always associated with at least some local (within 20 m) presence of *Pinus*, supporting the findings of Parshall (1999) who found that stomata presence is most closely related to *Pinus* presence within 10 to 20 m. This suggests they are useful indicators of local tree presence but a fuller study involving samples taken at a range of distances from trees would be required to further evaluate their sensitivity as an indicator. It is also possible that *Pinus* stomata were not preserved in large numbers at the locations sampled in this study for reasons connected with the sedimentary environment. This idea is supported by the occurrence of similarly low stomata counts in well-humified peat from cores taken from the same localities.

Occurrence of *Pinus* needles within the moss samples was often associated with the presence of stomata in the corresponding pollen sample, but it was not unexpected that the surface material should yield so few stomata, as pine needles are resistant to decomposition (Lowe and Walker, 1997). For peat samples where the degree of humification may have destroyed any needle macrofossils that were present, stomata should provide a valuable tool for identifying local *Pinus* presence.

iii) Sensing canopy openness from basin mires

RSAP was estimated at 800 m for basins of 60 to 100 m, which suggests that selecting coring sites with basins within this size range up to c. 1500 m apart will allow some degree of overlap in *Pinus* pollen source areas to be used to make inferences about the spatial distribution of open and closed areas. Small sites were not suitable for detecting openness, presumably due to the dominance of local *Pinus* pollen on the signal. It was not possible to estimate source area for larger sites, but it was possible to identify which sites were open by the low percentages of *Pinus* pollen. These results suggest that where *Pinus* is the dominant AP type, low percentages (< 15%) reflect regional *Pinus* pollen, but the source of this may be as close as 1 km from the sampling point.

The openness study was limited to a study of *Pinus* cover, as this is by far the most dominant canopy-forming tree in the reserve today. It would have been useful to have sampled openings within and at different distances from the few localities where mixed or *Betula* woodland occur to explore their effect on the pollen signal. Although this study suggests that it is possible to detect open areas at counts of *c.* 300 TLP, it is probably difficult to make quantitative inferences about *Pinus* abundance across an openness gradient at this scale. As Davis *et al.* (1991) discussed, prolific pollen producers with well-dispersed pollen such as *Pinus* are unlikely to show a distinct decline across a species boundary. Further noise will be introduced by structural differences in the canopy; a less dense canopy may actually produce more pollen per unit area than a denser canopy, as individual trees will receive more light and therefore flower more profusely. Such factors will almost certainly have had some effect on the spatial variability of pollen production that would not be detectable with the simple percentage cover measures used here. Similarly, it is difficult to assess the impact on the pollen signal of local presence of individual trees close to the sampling point; even if trees are recorded individually, pollen production is difficult to quantify (Birks and Birks, 1980) and is likely to vary from tree to tree, depending on factors such as size and condition.

iv) Minimisation of effort

Many of the pinewood communities have very similar pollen signals, and it may be that in order to differentiate between them, a non-AP pollen sum is required. For this project, which is aimed at reconstructing major landscape units, the time required to achieve this level of detail was not considered appropriate. As it was still possible to readily distinguish pinewood from mixed or birch woodland and open areas from closed areas at a count size of 150 grains, this was deemed acceptable for the approach taken. It is acknowledged that much higher counts would be needed if rarer taxa were to be used as indicators, *e.g.* of human activity or grazing. Similarly, when interpreting small changes in percentage pollen from the cores, it needs to be borne in mind that some of these may be an artefact of the low counts used. Where potentially important changes are seen, extra counting can be carried out.

Assessment of validity and usefulness of the approach

Both the community and openness studies demonstrate that it is possible to identify open communities from closed forest communities and pinewood from birch woodland at low pollen

counts. Stomata, where present, are a potentially useful indicator of local tree presence. For some communities with similar pollen signals, it may be worth exploring the potential of plant macrofossils through surface litter sampling (*e.g.* for *Vaccinium*), bearing in mind that sediments used for palaeoecological analyses may not contain identifiable plant remains of the required taxa.

For this study, a major limitation was that the surface samples used for community characterisation were not sufficiently representative. Using ten samples from within the same area probably revealed more about the pollen collecting properties of that individual area than the plant community it was selected to represent. It would have been more useful to collect individual surface samples from different examples of the main community types by sampling in different locations throughout the reserve, ensuring sufficient samples were collected to allow better estimation of variability in the pollen signal for each community type at the scale of interest. It was possible to establish that several of the areas sampled, and therefore possibly their respective communities, have different signals that can successfully be distinguished at low counts. Surface sampling could be useful interpretation tools for Caledonian pine forest but are likely to be of more relevance for communities from the recent rather than the distant past due to the extent of human modification of the landscape that is seen today (*e.g.* O'Sullivan, 1973a, 1973b).

The full range of plant communities suggested by existing fossil pollen diagrams from Abernethy Forest (*e.g.* Birks and Mathewes, 1978; O'Sullivan, 1974) is not present in the reserve today, and although more representative surface samples and macrofossil studies would be useful, for some fossil assemblages, there may be no modern analogues and in this respect the inferences that can be made from surface samples may always be limited. In chapter 4, the usefulness of pollen dispersal modelling for Caledonian pine forest is assessed, with a view to using models to interpret such assemblages meaningfully in terms of feasible landscape mosaics.

Chapter 4. Assessing the suitability of pollen dispersal and deposition models for use in Caledonian pine forest landscapes

Introduction

Pollen analysis has a long history as a tool for investigating long-term vegetation change, and from the outset its potential for use in the quantitative reconstruction of past plant abundance using fossil pollen records has been recognised (*e.g.* von Post, 1916 in von Post, 1967; Davis, 1963; Andersen, 1970). Such a tool needs to be based on a detailed understanding of the pollen-vegetation relationship, which can be studied both theoretically and empirically using modern pollen in conjunction with data on the surrounding vegetation. A key challenge in pollen analysis is to be able to separate the pollen which is derived from the vegetation around a site within a defined area of interest, from the 'background' pollen from beyond this area. Although the pollen-vegetation relationship is a complex one, simplified theoretical models have been developed that produce validated predictions for certain combinations of site and vegetation types (*e.g.* a small lake in closed forest).

Firstly in this chapter, the development of theories that attempt to give a more precise understanding of the pollen-vegetation relationship are reviewed, focusing on the Prentice-Sugita model of pollen dispersal and deposition (Prentice, 1985; Sugita, 1993, 1994) and the Extended R Value (ERV) pollen-vegetation calibration model (Parsons and Prentice, 1981; Prentice and Parsons, 1983). The concept of a 'relevant source area of pollen' (RSAP) for patchy landscapes is introduced. Next, the ERV model is applied to empirical modern pollen and vegetation data from Caledonian pine forest to assess its performance in Caledonian pine forest and estimate RSAP. This is an important step for identifying the spatial resolution possible for reconstruction and is used to inform site selection for palaeoecological sampling (see chapters 5 and 6). Finally, hypothetical landscapes are generated to explore the effect of changes in forest cover and opening size on RSAP, and the implications of the results for application of these models to reconstructing past landscapes are discussed.

Pollen-vegetation calibration

There are two main approaches to calibrating pollen data: the comparative approach and the representation or correction factor approach (Birks and Gordon, 1985). The most widely used

example of the comparative approach is the modern analogue technique, which is used for interpreting past assemblages from a range of fossil groups (*e.g.* Turner, 1964; Janssen, 1966; Tinsley and Smith, 1974; Andersen *et al.*, 1989; Räsänen, 2001). In pollen analysis it involves comparing modern pollen assemblages from known vegetation units (defined according to the scale of the investigation) with fossil assemblages, using numerical methods such as dissimilarity coefficients to identify the best match (Wahl, 2004). Where a match or minimum level of similarity is satisfied, it is assumed that an analogue for the past environment has been found. Wahl (2004) has discussed the problem of determining statistical cut-off levels to minimise false positive and false negative errors when analogue matching. However, past communities may not necessarily resemble any known modern assemblages (Delcourt and Delcourt, 1981) so the problem of how to interpret non-analogue communities remains. Such communities are commonly found in palaeoecology and are often linked to differing climatic conditions. Reconstructions using this method can therefore be performed with greater confidence if independent proxies for past climate can be obtained.

The second approach to pollen-vegetation calibration, the representation factor approach, is based on the fundamental assumption that the relationship between pollen and vegetation takes the form:

$$p = f(v) \qquad \text{(i)}$$

where p represents a given sedimentary pollen assemblage and v is the composition of the vegetation surrounding the site at the time of deposition. Since 1916, when von Post recognised that modern pollen assemblages varied systematically with the composition of the surrounding vegetation (von Post, 1967), this assumption has underpinned the development of most theories of pollen analysis. Von Post observed that some taxa were consistently under- or over-represented and a major challenge in pollen analysis since has been to obtain a more precise understanding of how vegetation is recorded by pollen assemblages (Jackson, 1994).

Early attempts at pollen-vegetation calibration focused on defining taxon specific calibration coefficients, known also as representation factors (R values) to enable pollen percentage data for each taxon to be expressed in terms of the abundance of a specified area of surrounding vegetation (*e.g.* Davis, 1963). However, R-values for individual taxa were hugely distorted by

the presence of pollen from outside a given fixed area around each site. The need for including a 'background' component in the models became clear, to enable separation of 'relevant' pollen originating from vegetation around the site, so Andersen (1970) refined the model to take the form:

$$y_{ik} = \alpha_i X_{ik} + \omega_i \qquad \text{(ii)}$$

where α_i and ω_i are taxon specific constants: α_i = relative pollen productivity for species i, ω_i = background term denoting pollen arriving from outside distance d for taxon i at site k (an influx term, measured in grains per unit area per unit time), y_{ik} = pollen influx (grains per area per unit time), X_{ik} = absolute abundance of taxon i within a fixed distance d around site k.

An additional complication was that pollen influx data, whilst being linearly related to absolute vegetation data, is extremely difficult to obtain, being highly variable within and between sedimentary basins with differential sedimentary processes contributing to the noisiness of the data (Maher, 1981: Davis *et al.*, 1984). However, the use of percentage or proportional data introduces the 'Fagerlind effect' (Fagerlind, 1952; Prentice and Webb, 1986), whereby a linear relationship between absolute variables becomes non-linear when they are expressed as percentages. For systems with three or more taxa, the pollen percentage of one taxon will in theory depend on not only its own abundance, but also that of one or more of the others (Prentice and Webb, 1986). Whilst the Fagerlind effect should not be significant if all taxon abundances are below 20 – 30 %, in practice this is not often the case, and influx cannot therefore be reliably inferred using linear regression. As percentage data is all that is available for most quantitative pollen work, an additional term was incorporated into Andersen's (1970) R-Value model to correct for the 'Fagerlind' effect; the model, with its 3 sub-models, is therefore known as the 'Extended R-value' (ERV) model (Parsons and Prentice, 1981; Prentice and Parsons, 1983). The ERV model corrects the non-linear proportional dataset to a linear form using an iterative approach to solving simultaneous equations.

The basic ERV model takes the form:

$$P_{ik} = \alpha_i v_{ik} f_k + z_i \qquad \text{(iii)}$$

where P_{ik} = pollen percentage of taxon i at site k, α_i = pollen productivity of taxon *i* relative to a reference taxon set at 1.0, v_{ik} = vegetation data for taxon *i* in the vegetation to distance *z* at site *k*, f_k = a 'site correction factor' for site *k* which is a function of all the α and ω values for all the taxa at site k (the formula for f_k varies between ERV sub-models; in sub-model 2 the correction factor is applied to P_{ik} not v_{ik}), and z_i = a corrected background component representing input of pollen beyond distance *z* (again the formula varies between ERV sub-models).

Two of the three sub-models were presented by Prentice and Parsons (1983), each of which uses different assumptions about background. In sub-model 1, background pollen is assumed to be constant when expressed as a percentage. In sub-model 2, it is assumed that the species specific background component is constant relative to total plant abundance. Sugita (1994) modified the ERV model to give sub-model 3, which assumes that absolute vegetation data (*i.e.* abundance) is available and therefore estimates a constant species specific background component.

However, in all the ERV sub-models, there are two unknown parameters in the equation, α and z, so an algebraic solution is not possible. However, a numerical estimate of their values can be made by setting up a series of simultaneous equations using all the known values of P_{ik} and v_{ik} for all taxa. This requires the value of α for one taxon to be set at 1 to serve as a reference taxon. It is preferable to select a mid-range taxon that is consistently present to allow relative values of α for all other taxa to be sensibly expressed. A series of iterations can then be carried out using all the known values for P_{ik} and v_{ik} and the 'best fit' set of estimates for the parameters determined using the Maximum Likelihood (ML) method identified by Fisher in 1912 (see Prentice and Parsons, 1983). The ERV sub-models are also presented in their inverse forms to enable past plant abundance to be estimated from pollen proportions following estimation of α and z (Parsons and Prentice, 1983).

Prentice and Parsons (1983) tested the models with empirical pollen and vegetation data from lakes within closed forest landscapes and produced α values that were consistent and z values that were similar in magnitude and ranking between models. The α and z values obtained for individual taxa were also consistent with qualitative information already known about pollen production and dispersal for individual taxa, suggesting that either sub-model could be used to produce vegetation reconstructions at a scale suitable for modelling ecosystem dynamics (Prentice and Parsons, 1983).

Pollen source area

Pollen source area can be defined theoretically in several different ways. For homogeneous vegetation, the 'characteristic source area' concept can be used, which predicts that the source area for a particular taxon will vary depending on the size and type of site as well as the properties of the pollen type (Jacobson and Bradshaw, 1981). Empirical evidence from openings in closed forest systems has supported predictions (Tauber, 1965) that smaller, heavier pollen types have smaller source areas, and larger basins have larger source areas (Jacobson and Bradshaw, 1981; Bradshaw and Webb, 1985).

However, most real vegetation is patchy in nature, so more recently there has been a move towards investigating the pollen-vegetation relationship for heterogeneous landscapes (Sugita, 1994; Broström, 2002; Bunting, 2002, 2003; Nielsen, 2003; Bunting *et al.*, 2004). In this type of landscape, the pollen-vegetation relationship is more complex so a different concept of pollen source area is required, the 'relevant source area of pollen' (RSAP). This was proposed by Sugita (1994), following an investigation into the problem of separating the local pollen signal pollen from the surrounding vegetation from 'background' pollen for heterogeneous landscapes. He carried out simulation experiments using the Prentice (1985) model for a series of hypothetical patchy landscapes. For each site type or assemblage, he found that there was a distance from the sampling point beyond which the curve from a plot of Likelihood Function score against distance from the sampling point reaches an asymptote. This can also be expressed as the distance from the sampling point beyond which correlation between DWPA and pollen loading does not improve. He concludes that provided the background pollen is consistent, information on vegetation abundance for the area within this distance is adequate to reflect vegetation composition, and terms this the 'relevant source area of pollen' (RSAP). Little further information about the linear relationship between pollen and plant abundance will be obtained by surveying the vegetation beyond this distance (Sugita, 1994).

Distance-weighting of plant abundance data is important to obtain the 'pollen's view of the landscape' as plants growing closest to the sampling point will have a greater influence on the pollen assemblage than those further away (*e.g.* Prentice, 1985; Prentice, 1986; Sugita, 1993, 1994).

The RSAP is important for assessing the appropriate spatial resolution at which reconstruction can eventually take place. By estimating RSAP, it is possible to identify a component of the pollen signal that is adequate to reflect the composition of the local vegetation. This may be as little as 30% to 40% and is superimposed on a consistent 'background' component common to all spectra from the region (Sugita, 1994). A combination of theoretical and empirical studies allows an improved understanding of the scale at which basins of different types and sizes reflect the surrounding vegetation, and RSAP has now been estimated for vegetation from North America using lakes (Sugita, 1994) and forest hollows (Calcote, 1995), and in Sweden and Denmark, also using lakes (Broström, 2002; Broström *et al.*, 2004; Nielsen and Sugita, 2005).

Factors that affect RSAP include the number of taxa analysed, vegetation patch size and distribution, wind speed and the method used for distance weighting of vegetation. These are discussed in detail by Nielsen (2003), who suggests that a larger RSAP may result from analyses using fewer taxa as this approach produces more similar composition across land cover classes, effectively making larger patches. She found little change in RSAP for varying wind speeds between 1 and 25 metres per second, and suggests this is because wind affects the background component of the pollen signal more than the local signal. Although a slight decrease in RSAP was noted at wind speeds below 1 metre per second, for Denmark, and certainly for upland areas in Scotland, such low wind speeds are so rare that in practice this is unlikely to have a significant impact on RSAP.

Modelling pollen dispersal and deposition

Several models have been devised in an attempt to explain how pollen assemblages form. Tauber's (1965) composite pollen transfer model, reviewed by Jackson (1994), proposed that pollen accumulating in a basin would be the sum of several components: a gravity component from overhanging plants or rainfall; a trunk-space component carried by low wind speeds below a forest canopy; a canopy component carried by wind above the canopy; a rainout component of pollen from the higher atmosphere and a waterborne component whereby pollen mainly from the watershed of the basin is transported in by inflowing streams or runoff (Tauber, 1965).

Faegri and Iverson's (1975) model was based on the assumption that convection causes the formation of a uniform pollen cloud, such that regional pollen signals would only vary according

to local anomalies. This is regarded now as untenable (Jackson, 1994), as its predictions are not borne out by empirical evidence.

Tauber's (1965) model has since become the basis for several conceptual models that attempt to predict pollen source areas. Jacobson and Bradshaw (1981) modified the Tauber model, changing the relative importance of the canopy, trunk space and gravity components for different sized basins. This correctly predicted an increase in pollen source area with basin size, but Jackson (1990) found empirical pollen assemblages to be less sensitive to local forest composition than would be expected if the trunk space and gravity components were important (Jackson, 1994).

From studies of basins in south east England, Bennett (1983, 1986) proposed that most pollen may reach lake basins via surface run-off and stream transport rather than via aerial transport, giving rise to a source area largely confined to the lake watershed. Jackson (1994) notes that this model is not consistent with other empirical observations that support the theory that pollen source areas differ between taxa according to their atmospheric dispersal properties (*e.g.* Bradshaw and Webb, 1985). He argues that waterborne transport may be dominant in certain situations, such as where there is a high watershed to lake area ratio or where permanent inflow streams exist, but maintains that atmospheric dispersal is the predominant mechanism for pollen to reach the land surface, so much of the pollen in streams must also derive from plants outside of the catchment area (Jackson, 1994).

Prentice (1985) presented a model of pollen dispersal based on Sutton's (1953) equation for the behaviour of particles released at or near ground level under stable conditions, which has been selected for modelling pollen dispersal and deposition for the following reasons. It can be regarded as so far the best available model for estimating pollen source areas in basins where atmospheric transport of pollen is dominant (Jackson, 1994), and many improvements in estimates of its parameters have been made in recent years (*e.g.* Sugita *et al.*, 1999; Nielsen, 2003; Broström *et al.*, 2004; Bunting *et al.*, 2005). The model compares well with empirical data, correctly predicting pollen source area for basins of differing size (Prentice, 1985; Bradshaw and Webb, 1985) and also reflecting the systematic differences in source area observed between pollen types (Jackson, 1990). The main assumptions are that the sampling basin is a circular opening, the dominant transport mechanism for pollen into a basin is via wind

above the forest canopy and gravity beneath the canopy, and that the pollen does not move once it is deposited on the bog surface. Also, the bog surface was assumed to be pure *Sphagnum*, so the influence of pollen from the local vegetation was not considered. Sugita (1993) modified the model for use with lakes, assuming complete mixing over the entire lake surface before deposition. The resulting Prentice-Sugita model effectively represents two extremes of a continuum from no post-depositional to complete post-depositional mixing (Jackson and Lyford, 1999); the reality for lakes is likely to lie somewhere in between, whilst for bogs it is likely that the assumption of the Prentice model is a reasonable approximation of reality.

Sutton's (1953) theory predicts that size and density dependent differences in fall speed will occur between different pollen taxa, with source areas increasing for larger, lighter particles. Hence, an emergent property of the Prentice-Sugita model is that the pollen source areas are specific to each taxon and will vary depending on the type and size of basin. This makes the model a useful tool for exploring the spatial properties of pollen assemblages. The quantity of pollen remaining airborne at a given distance from a point source is a function of the amount of pollen emitted by the point source, which equates to the relative pollen productivity of each taxon. This is estimated using the ERV model (Parsons and Prentice, 1981; Parsons and Prentice, 1983; Sugita, 1994).

As when estimating RSAP, vegetation data is incorporated into the model in a distance-weighted form to correct for the influence of plants close to the sampling point. Nielsen (2003) compared methods of distance weighting vegetation and found that the taxon specific approach of the Prentice-Sugita model makes the pollen-vegetation relationship most linear when distance from the basin centre is plotted against the Likelihood Function score obtained from the ML method. Un-weighted and inverse distance-weighted vegetation data show a decrease beyond a certain radius as plants from larger radii are included in the analysis, so can be considered less effective methods of estimating RSAP than the Prentice-Sugita model.

HUMPOL

HUMPOL (Hull Method of Pollen Simulation) is a recently developed software suite that can be used for simulating pollen dispersal and deposition using the Prentice-Sugita model and comprises several software elements. The scenario creation program Mosaic v.1.1 (Middleton and Bunting, 2004) is a powerful and flexible tool for generating hypothetical vegetation data.

This program allows scenarios to be modified in a controlled manner to explore the role of different model parameters (*e.g.* patch size, degree of openness, forest and ground vegetation composition and basin size/type). As well as being useful for hypothesis testing, such a tool can also assist with the design of sampling strategies, *e.g.* estimation of RSAP for different sizes of basin to explore the spatial sensitivity of a proposed network of sites. Mosaic v.1.1.produces an IDRISI format image, which comprises a grid of cells where each is assigned a value representing a plant community and an accompanying text file detailing cell size, dimensions of the array and geo-referencing information (Middleton and Bunting, 2004). The program PolGrid converts data from a variety of Geographical Information Systems (GIS) formats to the required IDRISI format allowing the Prentice-Sugita model to be used with empirical vegetation data (Bunting and Middleton, 2005).

The program PolFlow v.3.0 (Bunting and Middleton, 2005) applies the Prentice (1985) model of pollen dispersal for samples taken from moss polsters or a bog surface. (PolLake is the equivalent program for use with samples from lakes, which uses the Prentice-Sugita model). Vegetation maps are represented as grids of cells, each cell being treated as a pollen source with a positional component. This allows incorporation of position dependent factors, *e.g.* variable wind direction in the form of a wind rose. Incremental rings around each sampling point are defined by the user to enable calculation of DWPA. Vegetation maps of different resolution and spatial extent can also be nested to allow more detailed mapping of areas closer to the sampling point (Bunting and Middleton, 2005) and the inclusion of features that may occur in the wider landscape and exert an influence on the background component of the pollen signal (*e.g.* ecotones or large water bodies). The outputs from PolFlow (community composition by ring and simulated pollen counts) are then converted in PolLog for export into a spreadsheet such as Excel (for comparing simulated pollen counts with empirical pollen counts) or entered into PolERV for application of the ERV model, which in this case was used to estimate RSAP for both empirical and hypothetical pollen and vegetation data.

Using pollen dispersal models can be useful in several ways for understanding the landscape, but it is first important that results of simulations replicate empirical data. The Prentice-Sugita model has been shown to perform well for different combinations of pollen taxa and basin type or size (Sugita, 1994; Broström, 2002; Nielsen, 2004) and can be regarded as the best available model

for basins where atmospheric transport of pollen is dominant (see Jackson, 1994). Recent improvements in estimates of its input parameters have improved its performance further (*e.g.* Sugita *et al.*, 1999; Nielsen, 2003; Broström *et al.*, 2004; Bunting *et al.*, 2005). It was therefore decided to apply this model to simulate pollen dispersal and deposition in Caledonian pine forest landscapes and assess its performance against empirical pollen data. Since empirical pollen data were derived from samples collected from moss polsters rather than lakes, the Prentice model was used. This model was considered appropriate for studying the Caledonian pine forest as it has already been used successfully in semi-open cultural landscapes in North America (Sugita, 1994; Calcote, 1995) Sweden (*e.g.* Broström, 2002) and Denmark (Nielsen, 2003), but as yet little work has been done for semi-open landscapes in Britain.

Consequently, there are no published pollen productivity estimates (PPEs) for Scotland yet, but estimates for most major upland taxa are available from data collected in Sweden (Sugita *et al.*, 1999; Broström *et al.*, 2004). As pollen productivity may vary with geographical region, it was important to check the performance of the model using the available Swedish PPEs using with fossil pollen data for landscape reconstruction. Also, work to date has focused largely on lakes, which are relatively stable in size so the problems of changing RSAP associated with opening size changes over time are minimised.

In Scotland, there are fewer lakes that satisfy the size requirements for investigations into RSAP at a regional scale, but there are many suitable bogs. Using bogs reduces the problems associated with post-depositional mixing of the pollen signal as found in lakes, but does introduce additional complications at the reconstruction stage, in that opening size, and therefore RSAP, may have changed over time because of dynamic bog-forest margins. To some extent, the possibility of large changes in opening size having occurred in the past can be reduced by selecting coring sites from well-defined topographical basins, but it is still important to explore the possible effects of changes in opening size on the pollen signal. This can be carried out using pollen dispersal modelling. In this chapter, the effects of changes in opening size and forest openness on RSAP are explored through simulations using plant abundance data generated from hypothetical Caledonian pine forest landscapes.

Aims

The aims of this study are as follows:

i) to assess the performance of the Prentice model for Caledonian pine forest landscapes using empirical modern pollen and vegetation data

ii) subject to satisfactory performance, to use the model to estimate RSAP for a set of medium sized basins in Caledonian pine forest to assess the spatial sensitivity of the modern pollen signal

iii) to use the Prentice model with hypothetical landscape scenarios to investigate the effect of changing opening size and degree of openness on the pollen signal.

For i), the simulations were carried out in PolFlow using existing pollen productivity estimates for empirical vegetation data prepared in a GIS. Pollen deposition was simulated for sampling points corresponding to the locations of a set of modern surface samples. The simulated pollen assemblages were then compared with the empirical pollen assemblages to assess the performance of the model.

For ii), the ERV model was applied to empirical pollen and vegetation data using the program PolERV (see Bunting and Middleton, 2005), and Likelihood Function scores plotted against distance from source to obtain estimates of RSAP.

For iii), hypothetical landscape data was prepared with known forest cover and opening sizes using the scenario creation software Mosaic v1.1 (Middleton and Bunting, 2004). The ERV model was then applied and RSAP estimated as in ii).

Whilst it is desirable to run the simulations using the best vegetation data possible, in practice, this is often available only in a simplified form, particularly at larger scales. In this study, data from satellite imagery and detailed ground based surveys were used to produce three plant community classification schemes of varying complexity to investigate the effects of community classification on model performance.

Study area

Abernethy nature reserve, Inverness-shire, is a heterogeneous Caledonian pine forest and upland landscape that is owned and managed by the Royal Society for the Protection of Birds (RSPB). For full details of the study area, see chapter 1.

Methods

Sample collection

A sub-set of thirty moss samples (Set L_1)from the set of 119 surface samples collected from moss polsters in March 2003 (Set L) were used for this study, from locations 1, 2, 4, 10, 11 and 12 (Figs. 2.2 and 4.1). The sub-set comprised only those Set L samples from openings >30 m radius to avoid dominance of the signal by local (stand scale) pollen, thereby enabling subsequent investigations into pollen source area. A further 23 samples, also from openings > 30 m radius, were collected in March 2004 (Set SST; Fig. 4.1). Sample locations were geo-referenced using a Garmin handheld GPS. Samples from both years were collected and processed in the same way, from single polsters from within a circular area of *c.* 5 cm diameter as described in chapter 2. Pollen was extracted using standard methods (*e.g.* Moore *et al.*, 1991), and counted to *c.* 300 Total Land Pollen (TLP) grains at 400 x magnification. For details of all methods see chapter 2.

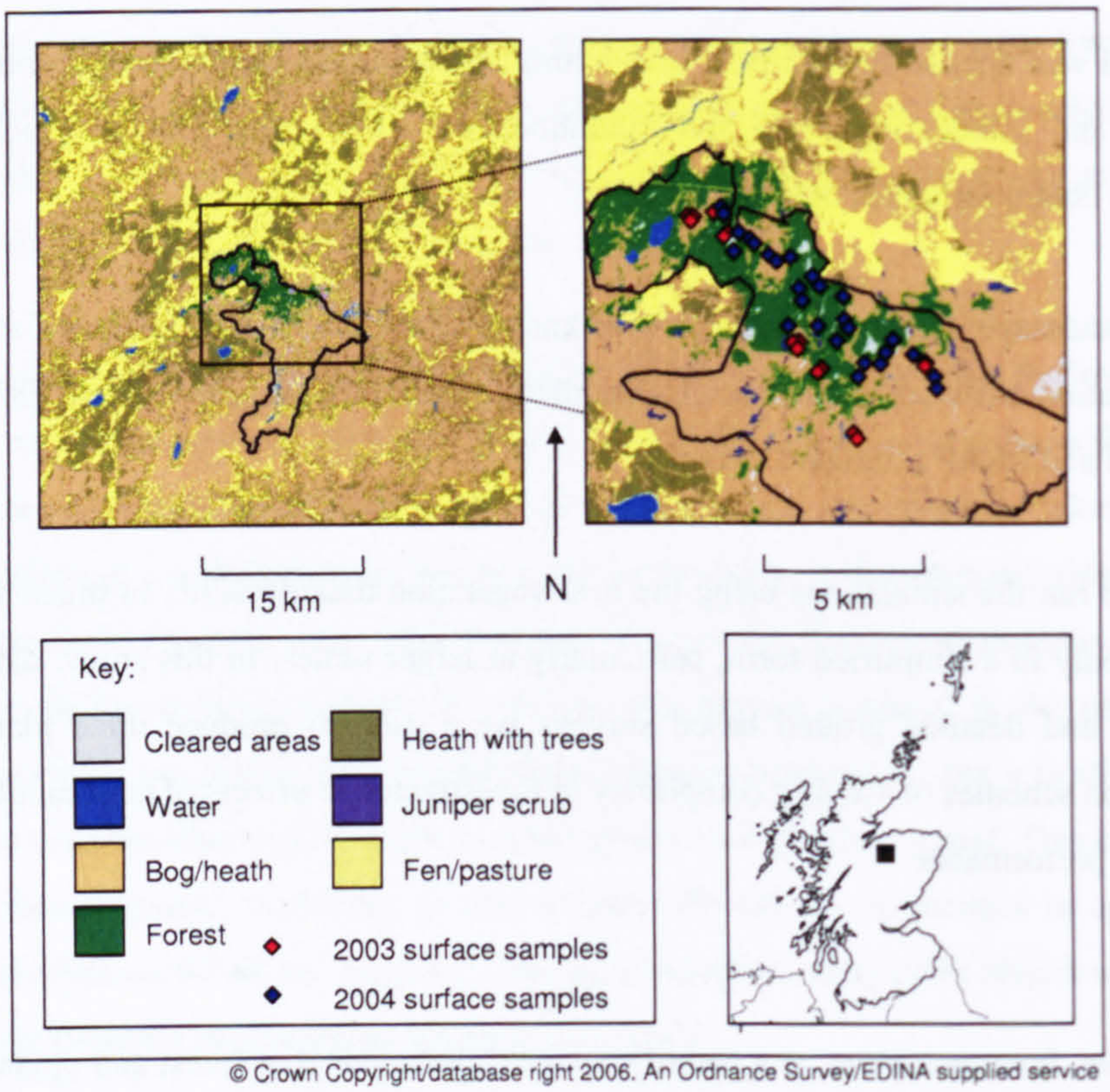


Fig 4.1. Location of Abernethy nature reserve (black outline), showing the area used for wider landscape (top left), the inner study area (top right) and the locations of set SST and set L_1 surface samples. Only major land cover types are shown.

Vegetation maps

Fully geo-referenced vegetation maps were prepared for later import into PolFlow from satellite imagery and National Vegetation Classification (NVC) and RSPB 2002 field survey vector map data for the Abernethy nature reserve. The wider landscape was mapped from a 51 x 51 km 100 m pixel resolution satellite image using RTManip v.5.0 (Middleton, pers. comm., 2003) to define a training set and reclassify the image into seven classes. For an inner study area of 15 x 15 km area centred on the reserve, the NVC and RSPB survey polygons were reclassified using a 20 community class scheme, simplifying information on species composition into palynologically equivalent taxa. ESRI ArcGIS v.9.0 was used to convert the maps from vector to raster form using a pixel resolution of 10 m (Fig. 4.1) to allow greater preservation of community detail than used for the wider landscape (Table 4.1).

Pollen productivity and fall speed estimates

Existing PPEs based on Swedish data (Sugita *et al.*, 1999; Broström *et al.*, 2004; Table 4.2) were used for all taxa except *Vaccinium*-type, which was derived from a Norwegian estimate (Hjelle, 1998). PPEs from Norfolk, UK suggest that *Alnus* pollen productivity for the UK may be higher than that of Sweden (for Swedish estimates, *Alnus*:*Quercus* = 0.55; for Calthorpe Broad, Norfolk, *Alnus*:*Quercus* = 1.39) so one of the simulations was also carried out using the UK *Alnus* value to assess its effect within the model. This was deemed necessary as the UK sample location more closely resembled the Scottish habitat and was wetter and further within the latitudinal range of *Alnus* (Grime *et al.*, 1988), than the open, better drained cultural landscapes of Southern Sweden. It was first necessary to adjust the UK *Alnus* PPE, as the average value used (Calthorpe Broad, UK; Bunting *et al.*, 2005) was expressed relative to *Quercus*, whilst the other PPEs being used were expressed relative to Poaceae. The average value for Calthorpe Broad was therefore raised relative to the Swedish PPE of 7.6 for *Quercus* (Sugita *et al.*, 1999) to give a ratio of 1.39, using the following calculation:

$$Alnus_{\text{PPE UKi}} / Quercus_{\text{PPE UK}} = 1.39/1.0 \quad \text{(iv)}$$

$$Alnus_{\text{PPE UKi}} / 7.6 = 1.39 \quad \text{(v)}$$

$$Alnus_{\text{PPE UKii}} = 10.56 \quad \text{(vi)}$$

with *Quercus* as the reference taxon in (iv) and Poaceae as the reference taxon in (v) and (vi). In the Norwegian data, with Poaceae as the reference taxon (Hjelle, 1998), *Vaccinium*-type PPE

was 0.04. However, *Calluna* was estimated at 0.95, so this was multiplied by a correction factor to harmonise it with the Swedish *Calluna* estimate of 4.7:

$$(4.7/0.95) \times 0.04 = 0.2$$

For fall speed, estimates used by Sugita *et al.* (1999) and Broström *et al.* (2004) were used, but as no published estimates yet exist for *Vaccinium*-type pollen, fall speed was calculated using Stoke's Law (Gregory, 1973):

$$v_s = \frac{2}{9} \frac{\sigma - \rho}{\mu} \cdot g r^2$$

where v_s = sedimentation velocity (cm s^{-1}), σ = specific gravity of sphere (g cm^{-3}, where water = 1.0), ρ = density of air (1.27×10^{-3} g cm^{-3}), g = gravitational acceleration (981 cm s^{-1}), μ = viscosity of air at 18° C (1.8×10^{-4}), r = radius of sphere (cm).

This satisfactorily predicts the fall speed of smooth spheres with a diameter of 1µm to 100 µm, and for pollen, has produced results that compare favourably with empirical observations. Radius (21.9 µm) was taken from the mean of measurements for *Vaccinium myrtillus*, *Vaccinium vitis-idaea* and *Arctostaphylos uva-ursi* as cited in Beug (2004). Pollen specific gravity was set at 1.0, on the basis that estimates for Angiosperm pollen fall within a narrow range of around this order (see Gregory, 1973, p21), and that the effect of specific gravity on fall speed is much smaller than that of particle size.

Data Analysis

Taxon selection and community composition

Three classification schemes for pollen taxa and community composition were designed for assessing model performance: i) 13 taxa, 12 communities, ii) 13 taxa, 18 communities and iii) a simplified 8 taxon, 6 community scheme (Table 4.1). In i), all pine forest was classed as 100% *Pinus*, whereas in ii), an additional five categories of *Pinus* forest were used, where *Pinus* was set at an arbitrary 90% to allow for a variable 10% field layer component . Using the software package PAST v.1.21 (Hammer *et al.*, 2004), these five categories were derived from cluster analysis performed on the RSPB 2002 field survey based on the relative proportions of *Calluna*, *Vaccinium*-type and Poaceae (Table 4.1, classes 10 to 15).

It is difficult to assess the potential pollen-producing biomass when considering different structural components of vegetation cover, so an arbitrary 10% of the mean percentage cover for each taxon in each cluster was assigned to field layer taxa, with the remaining 90% being assigned to *Pinus sylvestris* as canopy cover, as in terms of biomass this is by far the dominant species. These sub-classes were designed to enable a satisfactory level of detail for the study area to be preserved for exploring the contribution of pollen taxa from the field layer to the overall pollen signal. For all classes, the taxa selected were determined by the level to which different plant groups are readily identifiable by their pollen, *e.g.* all grasses were grouped as Poaceae. Herbs were treated as a single taxon on the basis that their productivities and fall speeds have a relatively small range; for these, an average derived from several palynomorphs was used. They were also treated as a group for data analysis as they occur in small percentages in both vegetation cover and pollen assemblages.

Table 4.1. Land cover classes (species data as percentage cover) to which vegetation data from the Abernethy Forest area were assigned for pollen modelling in HUMPOL. All available vegetation data was used for the 18 plant community system; for the 14 plant community system, pine forest field layer information was omitted (i.e. classes 10 to 15 were classed as 18) and for the 7 plant community system, all forest/field layer combinations other than birch woodland are classed as pine forest. In all cases classes 0 and 1 are non-pollen producing, so are excluded from the total number of plant communities.

Land cover no.	Land cover description	20 communities	12 communities.	7 communities	*Pinus*	*Betula*	*Picea*	*Corylus/Myrica*	*Alnus*	*Salix*	*Juniperus*	*Calluna*	*Vaccinium* type	Cyperaceae	Poaceae	Rumex	Herbs
0	Rock, settlement or clearfell	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
1	Water	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0
2	Open bog	2	2	2	0	0	0	0	0	0	0	35	5	55	3	0	2
3	Bog with scattered trees	3	3	3	20	0	0	0	0	0	0	25	5	45	3	0	2
4	*Carex* mire/fen	4	4	4	0	0	0	0	0	0	0	0	0	80	18	0	2
5	Open heath	5	5	5	0	0	0	0	0	0	0	60	30	0	5	2	2
6	Heath with scattered trees	6	6	5	10	0	0	0	0	0	0	58	25	0	3	2	2
7	Pasture, grazing or upland	7	7	7	0	0	0	0	0	0	0	0	0	0	95	2	3
8	Juniper scrub	8	8	5	50	0	0	0	0	0	25	20	0	0	5	0	0
9	Alder woodland	9	9	18	0	0	0	5	70	10	0	0	0	10	3	0	2
10	Pine forest with Grass	10	18	18	80	0	0	0	0	0	0	1	3	0	16	0	0
11	Pine forest with Grass/*Calluna*	11	18	18	80	0	0	0	0	0	0	5	0	0	15	0	0
12	Pine forest with *Vaccinium*/Grass	12	18	18	80	0	0	0	0	0	0	2	8	0	10	0	0
13	Pine forest with *Calluna*/ *Vaccinium*	13	18	18	80	0	0	0	0	0	0	8	8	0	4	0	0
14	Pine forest with *Vaccinium*	14	18	18	80	0	0	0	0	0	0	3	15	0	2	0	0
15	Pine forest with *Calluna*	15	18	18	80	0	0	0	0	0	0	14	5	0	1	0	0
16	Mixed woodland	16	16	18	20	65	0	3	10	2	0	0	0	0	0	0	0
17	Birch woodland	17	17	17	0	90	0	2	0	0	8	0	0	0	0	0	0
18	Pine forest	18	18	18	100	0	0	0	0	0	0	0	0	0	0	0	0
19	Pine/spruce plantation	19	19	18	50	0	50	0	0	0	0	0	0	0	0	0	0

Table 4.2. Fall speed and relative pollen productivity estimates for taxa used in land cover maps and simulations for Abernethy Forest. All values are relative to Poaceae, which is set at 1.0. Sources: *Broström *et al.*, (2004); **Broström (2002)***Sugita *et al.*, (1999); **** Nielsen (2003), ◊ modified from Bunting *et al.* (2005), † modified from Hjelle (1998) and ‡ this chapter. The two PPEs for *Alnus* are from Southern Sweden and Norfolk, UK.

Pollen type		Fall speed (m s^{-1})	Relative pollen productivity
***	*Pinus*	0.031	5.7
***	*Picea*	0.056	1.8
***	*Betula*	0.024	8.9
***	*Quercus*	0.035	7.6
***	*Corylus*	0.025	1.4
	Alnus	0.021	***4.2, ◊10.56
***	*Salix*	0.022	1.3
***	*Juniperus*	0.016	2.1
*	*Calluna*	0.038	4.7
	Vaccinium-type	0.058‡	0.2†
*	Cyperaceae	0.035	1.0
*	**Poaceae**	**0.035**	**1.0**
**	*Rumex*	0.018	4.7
****	Herbs	0.013	2.9

Pollen dispersal modelling

For each simulation using the three community classification schemes, the appropriate reserve scale vegetation map was loaded into PolFlow v.3.0, using the nesting function to place it within the larger 51 x 51 km map. Plant abundance (m^2) for each taxon was calculated for each of a series of incremental rings around a set of sampling points, set at 20 m width out to a radius of 2000 m. Sampling points were loaded as National Grid co-ordinates to match the locations of the surface samples taken. Wind speed was fixed at 3.0 metres per second for all analyses, as its effects were not under consideration in this study. The simulated pollen counts generated were compared with empirical modern pollen data for each of the three taxon/community classification schemes. For each community set, simulated and observed pollen proportions were plotted firstly by taxon and the strength of the relationships was assessed using the Pearson correlation coefficient (r) and the r^2 value using i) all 53 samples; ii) set L_1 (n = 30) and iii) set SST (n = 23). Simulated and observed pollen proportions were then compared by pollen

assemblage of each sample (n = 53) and classified using Ward's cluster analysis. The clusters were compared to assess how well the model replicated major vegetation units such as those identified in chapter 3.

Estimation of RSAP

Empirical percentage pollen data for 10 taxa in 7 communities from 40 surface samples comprising openings of similar size (c.50 x 50 m) was entered into PolERV together with plant abundance data (m^2). This was obtained from the empirical vegetation data using PolFlow and prepared for PolERV using PolLog (Bunting and Middleton, 2005). In PolERV, analyses were run for all ERV sub-models using Poaceae as the reference taxon. The Likelihood Function scores obtained were then plotted against distance from pollen source.

Investigating effect of basin size and openness on RSAP

Mosaic v1.1 (Middleton and Bunting, 2004) was used to generate simplified hypothetical landscapes based on a 5 km x 5 km area nested within wider 50 km x 50 km landscapes of similar vegetation pattern and community composition. These were used with the Prentice model to test the effects of opening size and changes in forest openness on RSAP. The vegetation community composition for these landscapes is shown in Table 4.3. For both 75% and 50% forest cover, scenarios were created with circular patches of bog vegetation of radius 30 m, 60 m and 100 m respectively, which were randomly located within the forest to act as sampling points at the simulation stage. Community composition for the 75% pine forest also comprised 1% birch woodland, 10% *Calluna* heath, 4% grassland and 10% bog, and for the 50% pine forest, 1% birch woodland, 30% heath, 9% grassland and 10% bog.

Three replicates were generated for each of the six openness/opening size combinations. Pollen for 23 sample points was then simulated for all replicates using PolFlow, and community composition was calculated for a series of 28 rings (10 m width out to 200 m then 100 m width out to 2000 m) around each sampling point. Both simulated pollen and ring community composition for each set of replicates were combined before performing ERV analyses on the six groups. Likelihood Function scores from the ERV analyses were then plotted against distance from source to locate the asymptote of the curve and thereby estimate the source area. The results were then compared across all six groups.

Table 4.3. Composition of simplified plant communities (species % cover) used in hypothetical landscapes for simulating RSAP.

Community	*Pinus*	*Betula*	*Calluna*	*Vaccinium*-type	Cyperaceae/Poaceae
Heath	10	5	45	30	10
Pine forest	80	0	10	5	5
Grassland	0	0	0	0	100
Bog	8	2	35	5	45
Birch woodland	0	80	10	5	5

Results

Relationships between observed and simulated pollen proportion by taxon

i) 13 taxon, 12 community scheme

Scatterplots of observed against simulated pollen proportions for 13 taxa and Poaceae combined with Cyperaceae are shown in Fig. 4.2, with set L_1 (2003) in red and set SST (2004) in blue. When samples from both years were analysed together, simulated and observed pollen proportions were significantly correlated for seven of the 13 taxa (Table 4.4). *Betula, Pinus, Alnus* and *Calluna* showed very strong positive correlations, at 0.99, 0.89, 0.81 and 0.87 respectively ($p<0.01$), and in all cases except *Alnus* the 1:1 fit was also good. In the case of *Alnus*, the model tended to under-simulate the proportion of pollen. Other positive correlations significant at the $p<0.05$ level were Poaceae (0.45), Cyperaceae (0.32) and herbs (0.32), which also showed reasonable fits to the 1:1 relationship between observed and simulated pollen proportions. Although the correlation coefficient was also significant for *Picea* (0.34), this taxon occurs in extremely low proportions in the observed pollen and not at all in the simulation. *Pinus*, *Calluna* and *Betula* show a relationship close to 1:1, and for Poaceae/Cyperaceae, predicted pollen is higher than observed for Cyperaceae and lower than observed for Poaceae. As both taxa are modelled with identical fall speeds and PPEs, they could also be analysed as a single taxon, which produces a better fit to the 1:1 relationship (Fig. 4.2).

When relationships between observed and simulated samples from 2002 and 2003 were analysed separately, *Pinus* and *Calluna* were significantly correlated in both years, but other taxa showed more variable relationships. There was a better correlation for Cyperaceae and *Vaccinium*-type in the 2003 samples, whilst *Picea*, and in particular, *Juniperus* and *Betula* were better correlated in the 2002 samples. Relationships between observed and simulated pollen proportions for *Rumex undiff., Salix* and *Corylus*-type were not significant in either year.

When the simulation was repeated using the UK *Alnus* estimate, the relationship between simulated and observed values for *Alnus* was still significant but the 1:1 fit remained poor. There was a slight decrease in the correlation coefficient r for all samples from 0.81 (r^2 = 0.66) for the Swedish PPE to 0. 77 (r^2 = 0.59) for the UK PPE. This appears to have been caused by the model predicting around 3.5 and 4.5 % *Alnus* pollen for just two samples from birch woodland where in fact, no *Alnus* pollen was seen (Fig 4.3b). Removal of these samples from the analysis produced a value for r of 0.83 (r^2 = 0.68), which is a slight improvement on the Swedish estimate. The use of the UK *Alnus* PPE had little effect on the relationships between simulated and observed pollen proportions for the other taxa, and Pearson correlation coefficients (and hence r^2) were of similar magnitude.

Table 4.4. Pearson's correlation coefficient and r^2 values for the relationship between observed and simulated pollen proportions for 53 sites at Abernethy Forest using a 13 taxon, 12 community system. Norwegian estimates were used for *Vaccinium*-type and Swedish estimates for all other taxa. Significance levels apply to Pearson correlation coefficient: *p<0.05, **p<0.01.

Taxon	Pearson correlation coefficient (n = 53)	r^2 for all samples (n = 53)	r^2 for all set L_1 (2003) (n = 30)	r^2 for all set SST (2004) (n = 23)
Pinus	0.89**	0.89	0.91	0.64
Picea	0.34*	0.13	0.13	0.10
Betula	0.99**	0.98	0.99	0.09
Corylus	0.06	<0.01	0.02	<0.01
Alnus	0.81**	0.66	0.05	0.97
Salix	-0.10	0.02	<0.01	<0.01
Juniperus	0.59**	0.34	0.51	0.03
Calluna	0.87**	0.77	0.87	0.70
Vaccinium type	0.19	0.04	0.01	0.23
Cyperaceae	0.32*	0.10	0.03	0.32
Poaceae	0.45*	0.21	0.06	0.59
Poaceae/Cyperaceae	0.34*	0.12	0.02	0.38
Rumex undiff.	-0.02	<0.01	<0.01	0.02
Herbs	0.32*	0.10	0.13	0.16

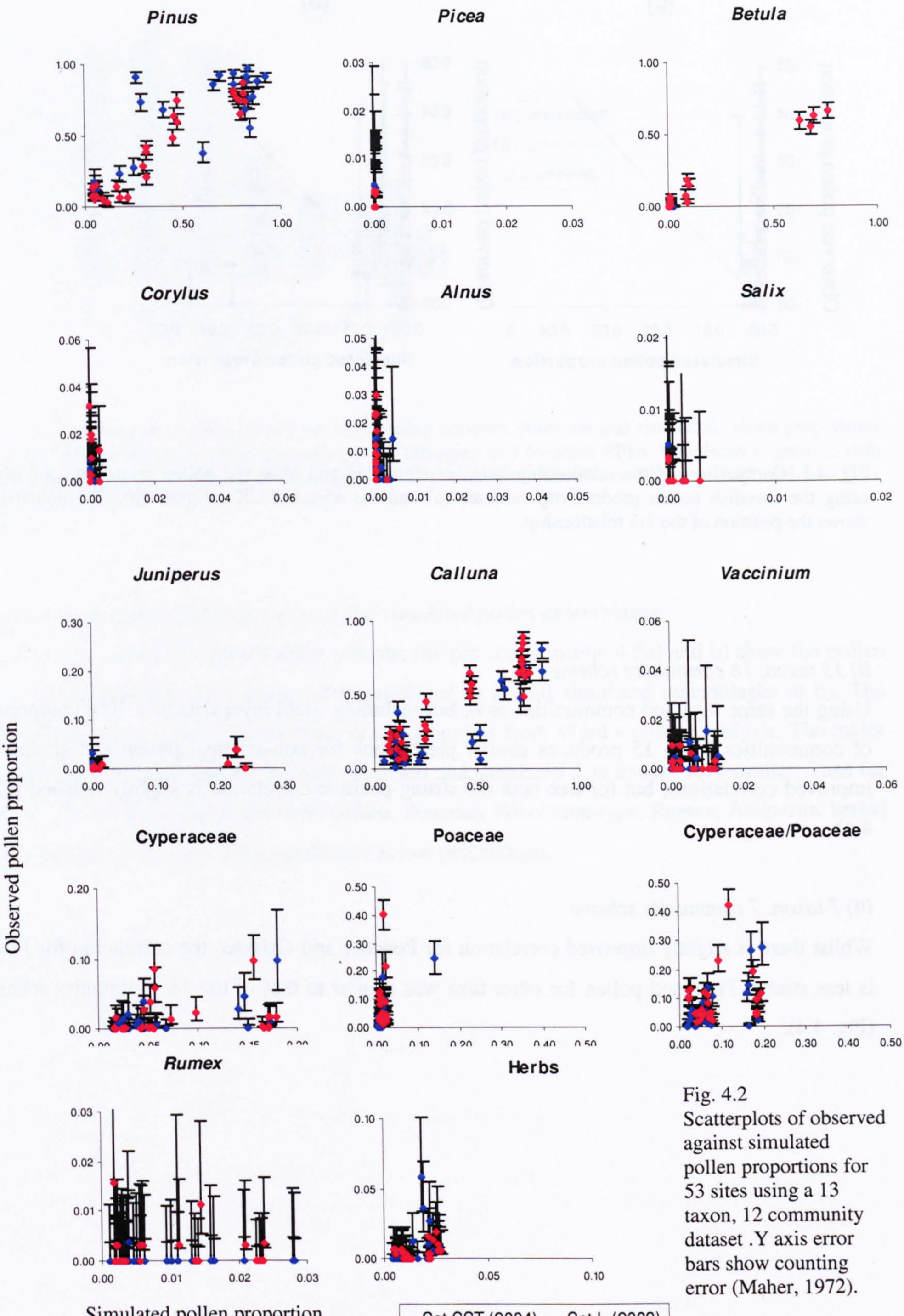


Fig. 4.2
Scatterplots of observed against simulated pollen proportions for 53 sites using a 13 taxon, 12 community dataset .Y axis error bars show counting error (Maher, 1972).

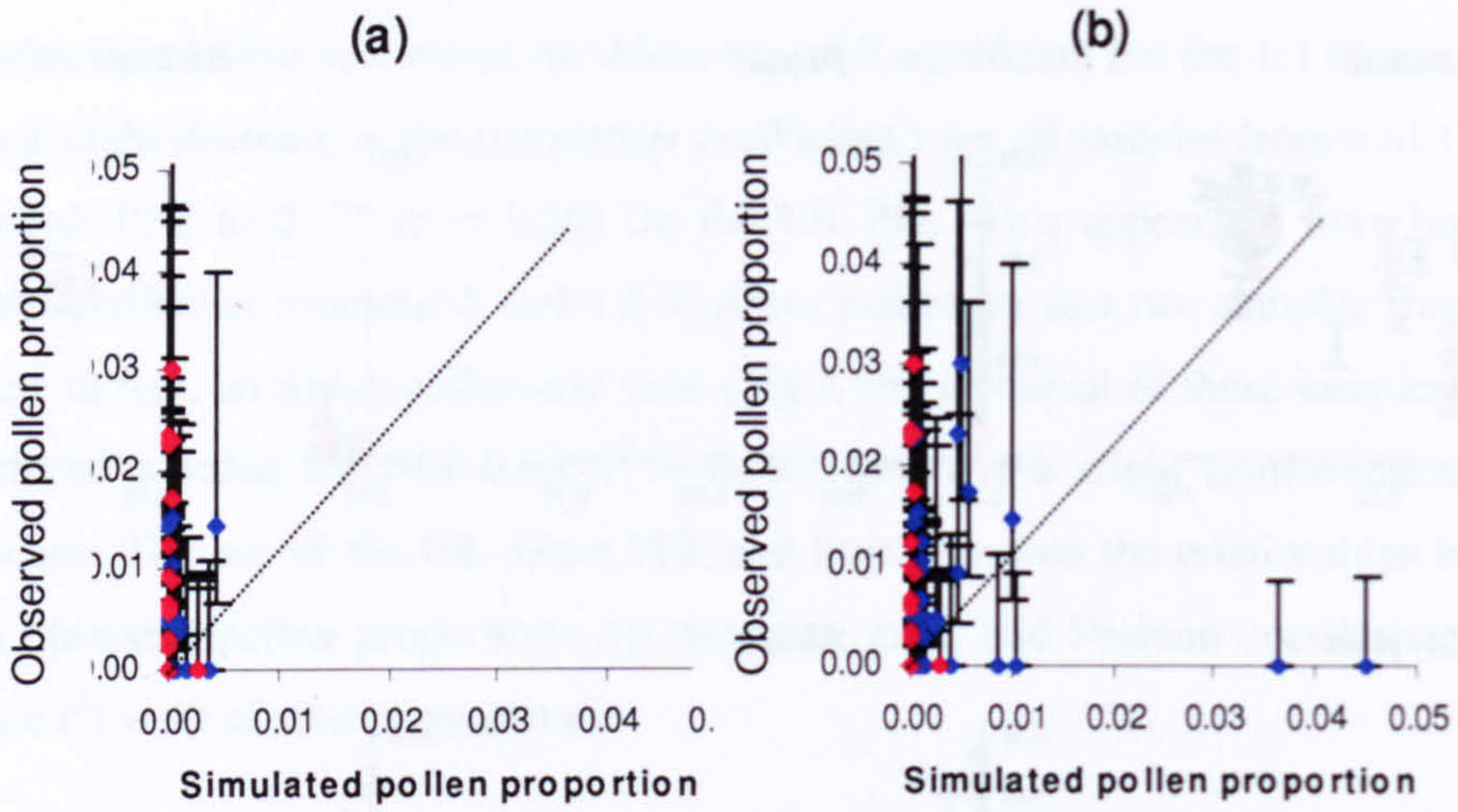


Fig. 4.3. Comparison of the relationship between simulated and observed pollen proportion for *Alnus* using the Swedish pollen productivity estimate (a) and the adjusted UK estimate (b). The dotted line shows the position of the 1:1 relationship.

ii) 13 taxon, 18 community scheme

Using the same taxa and communities as i), but including field layer data as a 10% component of communities 10 to 15 produces similar predictions for non-arboreal pollen and similar or improved correlations, but for tree taxa the strong positive correlation is slightly reduced (Fig. 4.4).

iii) 7 taxon, 7 community scheme

Whilst there is slightly improved correlation for Poaceae and *Calluna*, the correlation for *Pinus* is less strong. Predicted pollen for other taxa was similar to that of the 18 community scheme (Fig. 4.4).

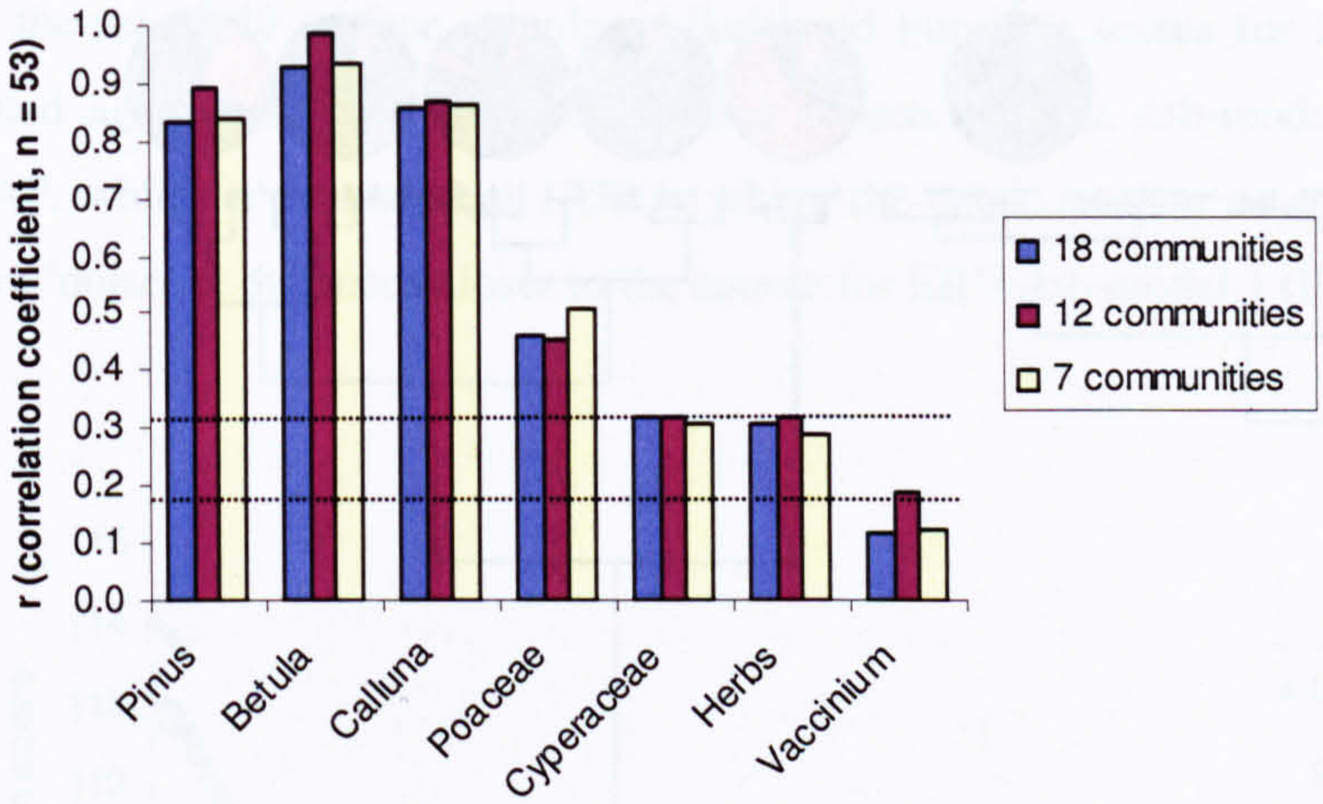


Fig. 4.4. Correlation coefficients for the relationship between observed and simulated pollen proportions for n = 53 samples for selected taxa using the Norwegian and Swedish PPEs. Simulated vegetation data was classified into 18, 12 and 7 communities. The horizontal lines show the p = 0.05 and p = 0.01 significance levels.

Comparison and classification of real and simulated pollen assemblages

For the 12 community classification scheme, the pie charts in Fig. 4.5a) and b) show the pollen data as assemblages, with observed assemblages in a) and simulated assemblages in b). The assemblages are grouped on the basis of dendrograms from Ward's cluster analysis. The major pollen assemblage groupings for both observed and simulated data appear very similar. Taxa for which the model predicted less well (*Alnus*, Poaceae, *Vaccinium*-type, *Rumex*, *Juniperus*, herbs) are those which occur in the assemblages at low percentages.

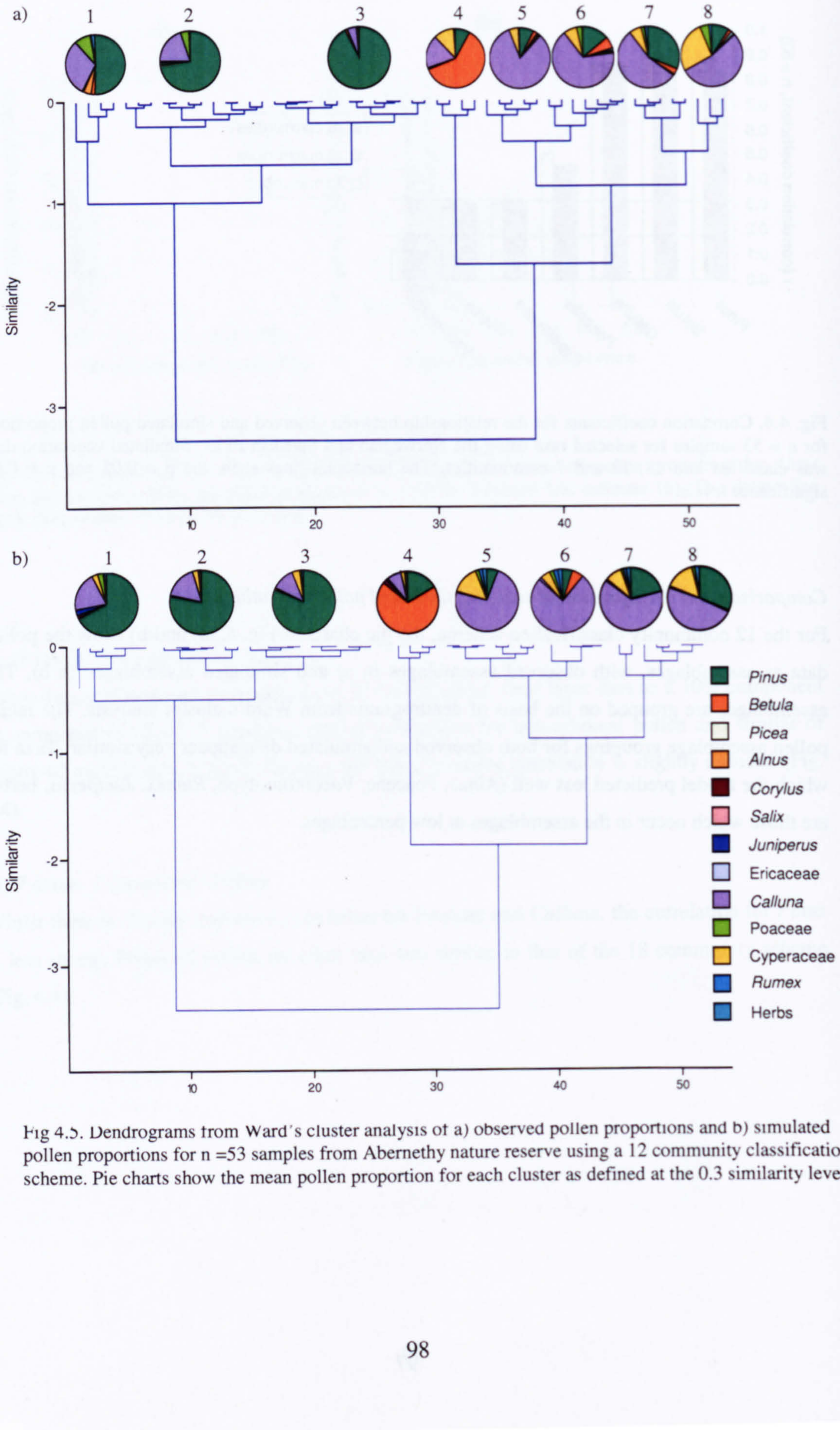


Fig 4.5. Dendrograms from Ward's cluster analysis of a) observed pollen proportions and b) simulated pollen proportions for n =53 samples from Abernethy nature reserve using a 12 community classification scheme. Pie charts show the mean pollen proportion for each cluster as defined at the 0.3 similarity level.

Estimation of RSAP

For the set of 40 surface samples, Likelihood Function scores for the 3 ERV sub-models are plotted against distance (m) from pollen source. All the sub-models give similar results for RSAP, which is estimated at 1050 m where the curve reaches an asymptote, although there is more 'noise' at distances closer to the source for ERV sub-model 1 (Fig. 4.6).

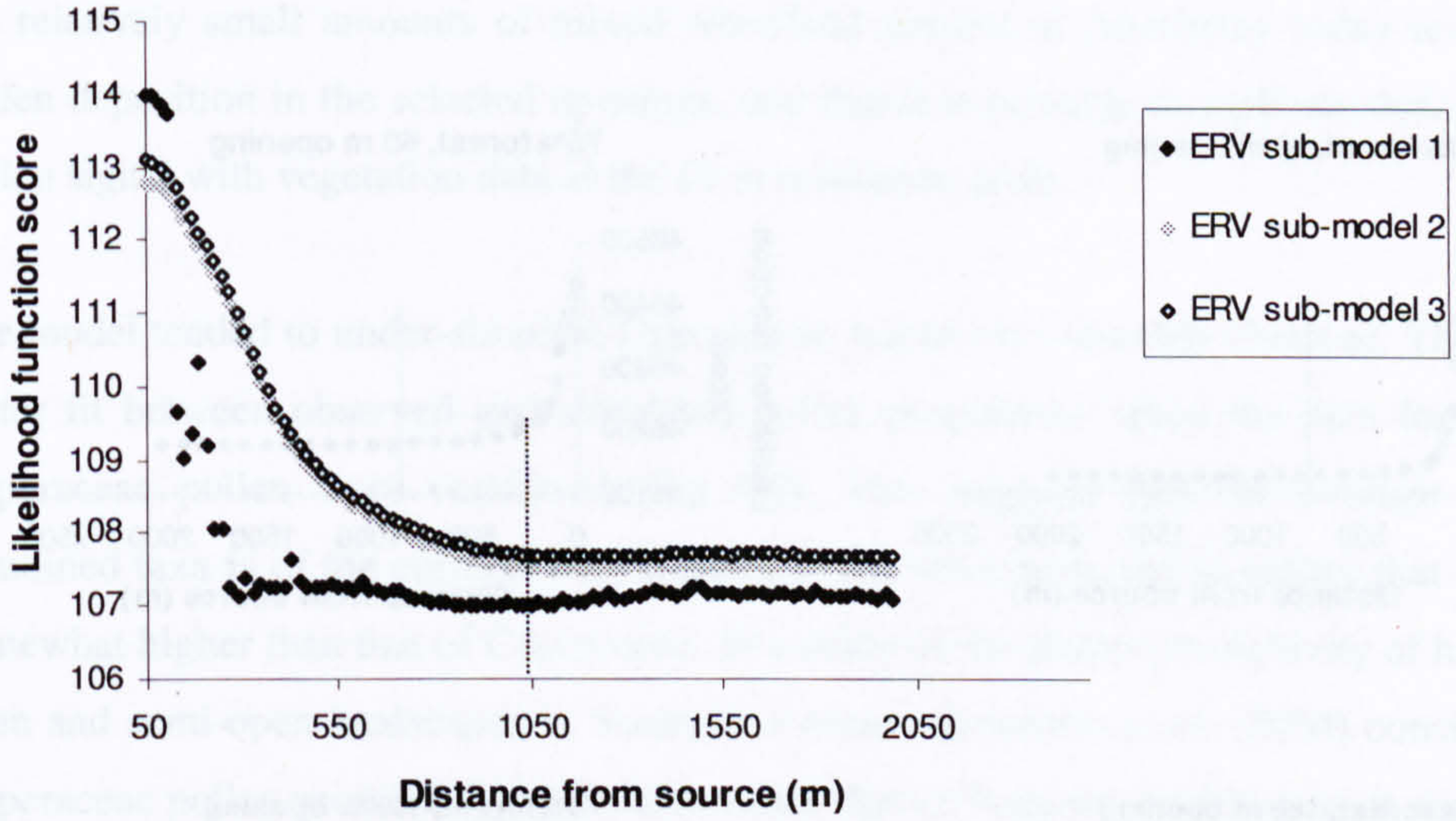


Fig. 4.6. Likelihood Function score plotted against distance from source using the three ERV sub-models, calculated using empirical pollen and vegetation data for 10 taxa from 40 sites. Relevant source area of pollen for all models is estimated at *c.*1050 m, shown by the vertical line.

Openness and opening size simulations

Plots of Likelihood Function score against distance for hypothetical landscapes with 75% and 50% forest cover with openings of 30 m, 60 m and 100 m radius are shown in Fig. 4.7. Each plot represents the combined results for three replicate scenarios, with a combined total of 69 sampling points. At 50% forest cover, the asymptote is reached and RSAP estimated at 600 m (30 m openings), 950 m (60 m openings) and 1200 m (100 m openings). A similar trend is seen at 75% forest cover: RSAP for 30 m and 60 m openings is estimated at 800 m, and for 100 m openings, 1200 m.

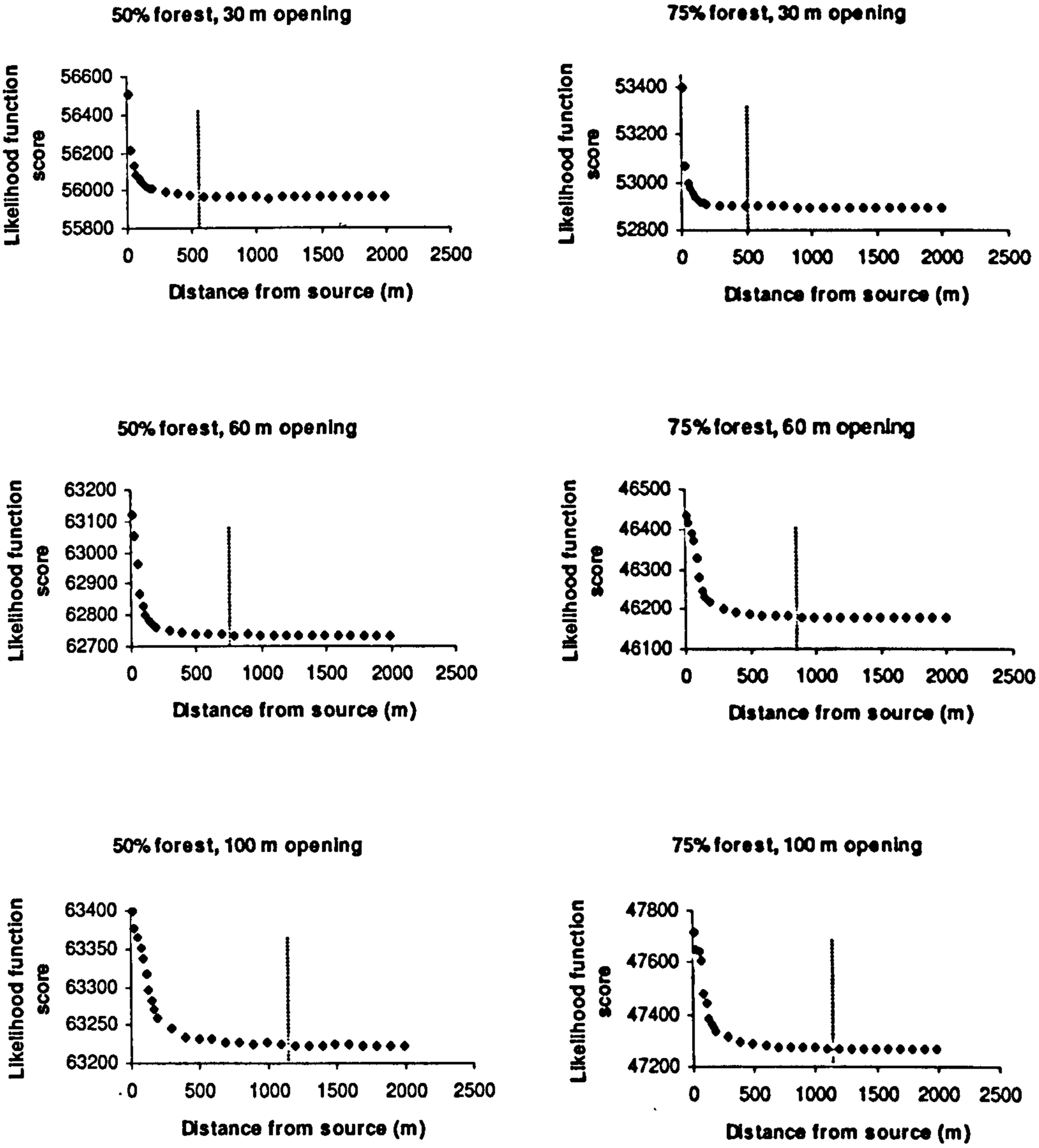


Fig. 4.7 Plots of Likelihood Function score against distance from basin centre for forest cover of 75% and 50% and opening sizes of 30 m, 60 m and 100 m radius. The dotted lines show the where the curves reach an asymptote, indicating the radius of the estimated relevant source area of pollen (RSAP).

Discussion

Significant positive correlations between observed and simulated pollen were obtained for seven major taxa, with particularly good model performance for *Pinus*, *Betula* and *Calluna*. This

suggests that the Prentice (1985) model is working sufficiently well to be applied in Caledonian pine forest to the reconstruction of major vegetation units comprising these taxa. Although the 12 community system performed marginally better, the results demonstrate that using a simplified 7 community system with the Prentice model can effectively reproduce modern pollen assemblages for this type of landscape. In the 7 community system, the relationship between simulated and observed *Pinus* pollen was less strong, most likely due to its being over-represented as a result of mixed woodland being re-classified as *Pinus* forest. This suggests that the relatively small amounts of mixed woodland present at Abernethy today are reflected in pollen deposition in the selected openings, and that it is possible to replicate their effect on the pollen signal with vegetation data at the 10 m resolution scale.

The model tended to under-simulate Cyperaceae, but to over-simulate Poaceae. There is a much better fit between observed and simulated pollen proportions when the data for Poaceae and Cyperaceae pollen were combined (Fig 4.2). This suggests that the average PPE for the combined taxa is of the correct order relative to the other taxa, but in reality that of Poaceae is somewhat higher than that of Cyperaceae. In a study of the pollen productivity of herb taxa from open and semi-open landscapes in Southern Sweden, Broström *et al.* (2004) consistently found Cyperaceae pollen productivity to be lower than that of Poaceae. In this case, it seemed sensible to treat Poaceae and Cyperaceae as a single taxon for several reasons: both taxa have grains of similar size and shape, so have similar fall speeds. As they both have the same PPE in the Swedish estimates, they are treated in the same way by the model. Also, it is often difficult to reliably estimate the relative proportions of these two taxa in the field, especially where they co-exist. Although this may be problematic for estimating PPEs when it is preferable that the vegetation survey is as accurate as possible, it is of less importance for this type of study where both taxa occur in similarly open land cover types at a landscape scale.

A combination of factors was likely to be operating for other taxa where the model failed to predict satisfactorily. Since only a 10 m resolution vegetation dataset was used, some of the variability in the observed pollen signals can be attributed to local presence of plants that would not have been recorded at this scale. It is also difficult to assess model performance with respect to taxa occurring at low percentages in the empirical data (*Picea*, *Rumex undiff.*, herbs), or for those such as *Vaccinium*-type that are under-represented in the pollen record due to low

productivity (*cf.* Tinsley and Smith, 1974) or poor preservation, such as *Juniperus* (Moore *et al.*, 1991).

The variable results for *Alnus*, *Salix* and *Corylus*-type may be linked to the fact that these are infrequent or of restricted distribution in the present vegetation. For *Alnus*, the large variability in observed pollen is likely to be related to its high productivity and localised riparian habitat (Bunting, 2003), as under these circumstances the pollen signal is likely to be more vulnerable to the effects of annual or stand scale variations in pollen production . The difficulties of modelling the pollen-vegetation relationship for these taxa present challenges for past reconstruction; *Alnus* and *Corylus*-type in particular are often important components of fossil pollen diagrams.

To some extent the effects of annual or local variability can be minimised at the sampling stage by amalgamating moss polsters collected for pollen productivity estimation (*e.g.* Broström *et al.*, 2004). PPEs may also vary geographically or between habitats (*e.g. Alnus*; Bunting, 2005), which can be problematic. As was the case with the UK *Alnus* and relative Cyperaceae/Poaceae estimates in this study, PPEs from different regions may be unsuitable, giving simulated pollen loadings that over or under-represent particular taxa. Without further PPEs for different habitats and regions, the extent of this effect is difficult to establish. In addition, when used for simulations designed to be compared with fossil data, there is an assumption that these values have not changed significantly over time.

For herbaceous taxa, it is difficult to estimate percentage cover at larger scales and generally, these taxa can be modelled more effectively at smaller scales (*e.g.* Hjelle, 1997, 1998, 1999; Bunting, 2003). Even at small scales, small components of the vegetation may, depending on the time of year, be over or under-estimated during the vegetation survey stage. In this study, the poor predictions for *Rumex undiff.* are most likely to be a result of attempting to model a small, locally frequent species at too large a scale. In addition, the Prentice model, being based on Sutton's (1953) equation, assumes that all pollen enters the atmosphere at ground level. This may be a valid model for arboreal taxa in closed forest situations where height and continuity of cover are relatively consistent, but there will be different mechanisms of entrainment for pollen from different structural components such as herbs and shrubs; for these, the pollen is released close to the ground where low wind speed may inhibit dispersal (Solomon and Harrington, 1979;

Nielsen, 2003). Nevertheless, the Prentice model performed well for *Calluna* and Cyperaceae/Poaceae, suggesting these issues become more important at smaller scales.

Addition of data relating to the field layer does not improve the performance of the model, in particular for tree species. This supports the idea underpinning the Prentice model that the dominant mode of pollen transport is by wind entrainment above the canopy, with canopy throughfall forming a minor component of the pollen signal. The results obtained from these simulations suggest that for the sites chosen, the estimate of a 10% field layer component to 90% canopy is probably too high. If this is the case, it is likely that differences in pollen productivity related to *Calluna* under the canopy flowering less under the canopy than in open situations (Iason and Hester, 1993) will have little impact on the pollen assemblages of samples taken from openings > 30 m radius, where the signal is not likely to be dominated by local pollen. No account was taken of the possible existence of 'edge effects' around the *Pinus* canopy, whereby flowering may increase where the sides of trees receive more light. However, as there was an excellent fit between observed and simulated *Pinus* pollen, this effect cannot be assumed to be of great importance at this scale.

This work has also shown that different results may occur where moss polsters are sampled in different years. This supports the findings of Räsänen *et al.* (2004), who suggest that mosses may only contain a record of between one and two years' pollen accumulation (see chapter 2). These differences may be a reflection of actual differences in pollen deposition caused by factors such as differences in recent weather conditions, but as the same sites were not sampled between years it was not possible to separate site factors from environment-related factors. The variability in the results presented here does serve to emphasise the importance of developing consistent methodology for both vegetation survey and moss polster sampling when carrying out this type of work.

When analysing the ability of the model to replicate the pollen assemblages from the 53 sample points, the results were more promising with regard to reproducing the major landscape elements present today. These were clearly differentiated by cluster analysis on the basis of pollen percentages from a few taxa: *Pinus*, *Calluna*, *Betula* and Poaceae/Cyperaceae. As the poorer predictions were for those taxa that occurred at very low percentages, these had little overall influence on the clustering. Identification of these major vegetation units suggests that

reconstruction of past vegetation at the intended scale is feasible using simplified vegetation communities with as few as four or five taxa, taking account of pollen taxa with similar characteristics that may be grouped.

However, the poor performance for *Corylus* and *Alnus* is potentially problematic, as fossil pollen assemblages suggest that these were important components of past vegetation (see chapters 5 and 6). One possible solution for *Corylus* is to model it as part of a mixed *Betula/Corylus* community and use a combined *Betula/Corylus*-type pollen taxon. Existing pollen evidence from Abernethy Forest suggests these taxa once existed in close association at low altitude parts of the forest (*e.g.* O'Sullivan, 1974, Birks and Mathewes, 1978). Ideally, further work in parts of the Scottish Highlands where these taxa are more abundant would be required, with a view to estimating relative pollen productivities for Scotland as well as assessing the model against pollen spectra from a wider variety of plant communities.

For openings of 60 to 120 m radius, the estimated RSAP of 1050 m for the present day suggests that, subject to considerations of possible changes in opening size, the pollen signal reflects the surrounding vegetation at a useful scale for reconstruction for this size of opening. This is slightly higher than the RSAP estimate of 800 m for *Pinus* obtained in chapter 3 from the correlation of percentage *Pinus* pollen with *Pinus* abundance ($1/d^2$).

The simulations produced similar RSAPs for both 50% and 75% forest cover, with estimates for the radius of the RSAP increasing as opening size increased, as theory predicts (*e.g.* Prentice, 1985; Sugita, 1994). The relatively small increases in RSAP observed suggest that its radius may not change by more than two hundred metres or so for openings within the size range of 30 m to 100 m radius. Changing the amount of forest cover seemed to have very little effect, but the effects of landscape pattern were not considered here, and other simulations suggest that such effects have a significant influence on RSAP (Bunting *et al.*, 2004). Although these were hypothetical landscapes, they can give a general indication of suitable criteria for site selection. In this case, sites with well-defined basins within a 30 m to 100 m radius appear to be well-suited for reconstruction. On the basis of the RSAP estimates, sites between one and two kilometres apart should have overlapping source areas, which is a useful finding for the palaeoecological site selection stage.

Quantitative vegetation reconstruction is still work in progress and the need to explore the effect on pollen dispersal and deposition of potentially important factors, such as landscape pattern (Bunting *et al.*, 2004), topography, prevailing winds and irregular lakes (Bunting and Middleton, 2005) is currently being addressed. It is perhaps also worth noting that there are many stages at which error can be introduced, so it is important to be able to identify and quantify it as far as possible, in proportion to the time this would inevitably remove from other areas of work.

Whilst pollen analysis has been shown to work well for describing vegetational change over long periods, there is still a need to consider sampling, preparation and counting errors (Tipping, 1994). For samples collected from moss polsters, there may be fewer problems relating to the post-depositional environment, but there is still a lack of standardisation at the sampling stage which may affect the composition of the pollen assemblage. This issue has only recently begun to be redressed (*e.g.* Jackson and Wong, 1994; Hicks *et al.*, 1998; Räsänen *et al.*, 2004). Undoubtedly the lack of standardisation has contributed to conflicting views about how many years of pollen deposition are represented in moss samples. Similarly, there is as yet no accepted set of procedures for vegetation survey, particularly in relation to small scale (0-50 m) mapping and for estimation of PPEs. This is particularly important for PPEs, where establishing geographical and habitat dependent variations in productivity is likely to be an increasingly important requirement for large scale studies.

Improved estimates for these input parameters for a wider range of taxa should allow better assessment of model performance across a wider variety of landscape types. In addition, if inter-disciplinary research aimed at developing and applying these techniques to specific questions of ecological relevance is to progress (*sensu* Birks, 1993, 1996), it will be useful to have some common standards for vegetation survey, palynological techniques and data analysis. Meanwhile, the results of this study suggest that the Prentice model is valid for use with fossil data for the process of reconstruction of past Caledonian pine forest landscapes using available pollen productivity estimates.

Chapter 5. The long-term history of Abernethy Forest: two new tephra-dated profiles

Introduction

Although several regional studies from large lakes or lake margins were published for Abernethy Forest in the 1970s (Birks, 1970; O'Sullivan, 1974a, 1976; Birks and Mathewes, 1978), the analysis of charcoal was not then routine. Long-term fire history for the reserve is therefore unknown and nor have there been any studies of fire history in the Cairngorms since (Bennett, 1996). The aim of this chapter is therefore to i) obtain information on long-term regional vegetation dynamics, including the role of fire and human activity in the landscape, and ii) provide a regional context for vegetation and fire history within which to interpret palaeoecological records from a network of smaller basins (see chapter 6). This was carried out by the collection and interpretation of two long-term regional palaeoecological records for Abernethy Forest, which are correlated with the previously published regional studies referred to above. Holocene vegetation history of the Central Highlands region and the Abernethy nature reserve is first reviewed to provide a context for subsequent interpretation.

Vegetation history of the Central Highlands

Early research into the post-glacial vegetation history of Scotland has been reviewed by Bennett (1996) and Huntley *et al.* (1997) and is discussed in chapter 1. In the Central Highlands region, there is a long history of continuity of forest cover and the forest, although much modified, is probably less affected by human activity than natural woodland elsewhere in Britain (Mackenzie, 2002). Pollen and macrofossil evidence from lake sediments and peat bogs have suggested that *Betula*, *Salix* and *Juniperus* were early colonisers after the last glacial retreat, arriving around 10,500 cal. BP (9500 BP) (Birks, 1989). From regional pollen records at Loch Garten and Loch a'Chnuic, the vegetation is thought to have been quite open at this time, with a mosaic of trees, grass and heath communities (O'Sullivan, 1974a). Pollen records from these and other profiles from the region (Vasari and Vasari, 1968; Birks, 1970; 1975) suggest that *Juniperus* scrub developed into dense *Betula/Corylus* woodland.

Gordon (1993) noted that the rapid rise to dominance of *Pinus* appears fairly consistent across the Cairngorms, with comparable radiocarbon dates between sediment profiles and

fossil *Pinus* stumps. Age estimates range from *c.* 8300 cal. BP (7400 BP) for pine stumps on the Cairngorms (Dubois and Ferguson, 1985) to *c.* 7550 cal. BP (6600 BP) for the completed rise of percentage *Pinus* pollen at Loch Pityoulish (O'Sullivan, 1976). A similar *Pinus* zone has been found in other cores from the Cairngorm area (Allt na Feithe Sheilich and Loch Einich: Birks, 1975) and Speyside (Loch Garten, Loch a'Chnuic and Loch Pityoulish: O'Sullivan, 1974a, 1975, 1976). The forest probably reached its maximum extent between *c.* 7800 to 5700 cal. BP (7000-5000 BP), but there were probably always open areas in the montane parts of the Cairngorms, with the main forest comprising *Betula* and *Pinus*, with *Alnus* on richer river valley soils. However, there is no direct palynological evidence at sufficient resolution to support these ideas (Mackenzie, 2002). In addition, the pollen record is likely to have under-represented *Pinus* growing close to its altitudinal limits, as such trees are often stunted and non-flowering (Bennett, 1996).

The altitudinal limit of *Pinus* seems to have varied during the Holocene. In a lake profile from Allt an Aghaidh Mhillis in the south east Cairngorms, Allen and Huntley (1999) found intermittent occurrences of *Pinus* and *Betula* macrofossils at an altitude of 880 m, which eventually disappeared from the record. They infer that the elevation of the tree line had fluctuated since 4600 cal. BP (4000 BP), with substantial open areas at higher altitudes, before more recent losses in upper forest cover in the region. They also found a reduction in *Betula* and *Pinus* macrofossils from a lake sequence from nearby Lochan Oir (500 m), where they suggest a maximal tree line at 5100 cal. BP (4500 BP) was in decline by 5000 cal. BP (4400 BP) (Huntley *et al.*, 1997; Allen and Huntley, 1999). This is consistent with other evidence for forest decline in the region at this time (Birks, 1975; Bennett, 1996; O'Sullivan, 1974a, 1975, 1976). Pears (1967) studied modern tree lines in the Cairngorms and identified anthropogenic factors such as grazing and felling as being responsible for an artificially lowered tree line since at least medieval times. McConnell (1996) studied pollen profiles above and below the only apparent example of a natural tree line in the Cairngorms today at Creag Fhiaclach, and concluded that it has been relatively stable at *c.*650 m asl since at least AD 1010. Evidence from fossil stumps has been recovered from altitudes up to 730 m asl in the Cairngorms (Dubois and Ferguson, 1985) but this is likely to reflect the preservation properties of the peat rather than the upper limit of tree growth (Huntley *et al.* 1997). Although not part of this study, there is scope for further work using pollen and *Pinus* stomata to investigate changes in the tree line in the Cairngorms.

The arrival of *Alnus* is regarded as a key event for the mid-Holocene (O'Sullivan, 1977), and its first appearance in the Cairngorms has been dated at *c.* 7500 cal. BP (6500 BP), which

coincides with the *Pinus* pollen maximum for several sites in the Scottish Highlands (see Pennington *et al.*, 1972; O'Sullivan, 1974a, 1976). It is likely that *Alnus* initially colonised wet lowland habitats such as the Spey valley (Birks, 1970), with the main increase in the percentage pollen record dated to between 6700 cal. BP and 6400 cal. BP (5900 BP-5500 BP). The main increase in *Alnus* pollen percentages at Abernethy Forest occurred by *c.* 6700 cal. BP (5900 BP), rather earlier than for elsewhere in the region (Birks, 1970; Birks and Mathewes, 1978). *Alnus* occurs in quite low proportions, implying that it was never present in any abundance despite rapidly colonising its eventual niche (Birks, 1970; O'Sullivan, 1977). Unlike *Betula* and *Pinus*, its seed is not wind dispersed and several mechanisms for its rapid spread into the Central Highlands have been proposed, including bird and animal activity, water transport and human agency (Chambers and Elliot, 1989).

Evidence so far suggests that the period of *Pinus* dominance lasted from *c.* 7800 cal. BP (7000 BP) until inferred human forest clearances at Loch Garten *c.* 3900 cal. BP (3600 BP) and later at Loch Pityoulish *c.* 3000 cal. BP (2900 BP) (O'Sullivan, 1974a; O'Sullivan, 1976). Following these early clearances, O'Sullivan (1976, 1977) suggested the surrounding landscape was one of *Pinus/Betula* forest with heathland. The significant changes occurring throughout Scotland around 4600 cal. BP (4000 BP) coinciding with the 'pine decline' and inception of blanket bog (see chapter 1) may not have affected the Cairngorms region as extensively as they did the north and west of Scotland. Mackenzie (2002) suggested that the chief impact of climate deterioration may have been a lowering of the tree line resulting from increased periglacial conditions in the montane zone, but Birks' (1975) study of pine stumps in the Cairngorms found no evidence for a synchronous decline, with both waterlogging and fire being identified as causes of tree death. Local variations in hydrological conditions may have contributed to a variable response to climate change across the region, and the effects of increased *Calluna* growth and the role of fire may also have been important factors. These are also linked to climate change but raise the additional question of human influence, which O'Sullivan (1977) argues was a more instrumental factor in the decline of the forests of the Central Highlands. However, it is difficult to evaluate the role of fire and its possible links to human activity in the absence of long-term charcoal records for the region.

Several profiles from the region including Loch Einich (Birks, 1975), Loch Garten and Loch a'Chnuic (O'Sullivan, 1974a) show a continuous, if slightly fluctuating, record of *Pinus* pollen from 7800 cal. BP (7000 BP) to the present, with apparent recovery of the forest following the first relatively small scale clearances *c.* 3900 cal. BP (3600 BP). The impact of

humans on the forest is still subject to debate. One view is that in some areas, the forests of the Cairngorms survived relatively intact until about 300 to 400 years ago (see O'Sullivan, 1974a; Mackenzie, 2002). However, historical map evidence for the Strathspey area suggests a more open cultural landscape was well-developed by AD 1600 (Smout, 1997; see chapter 1).

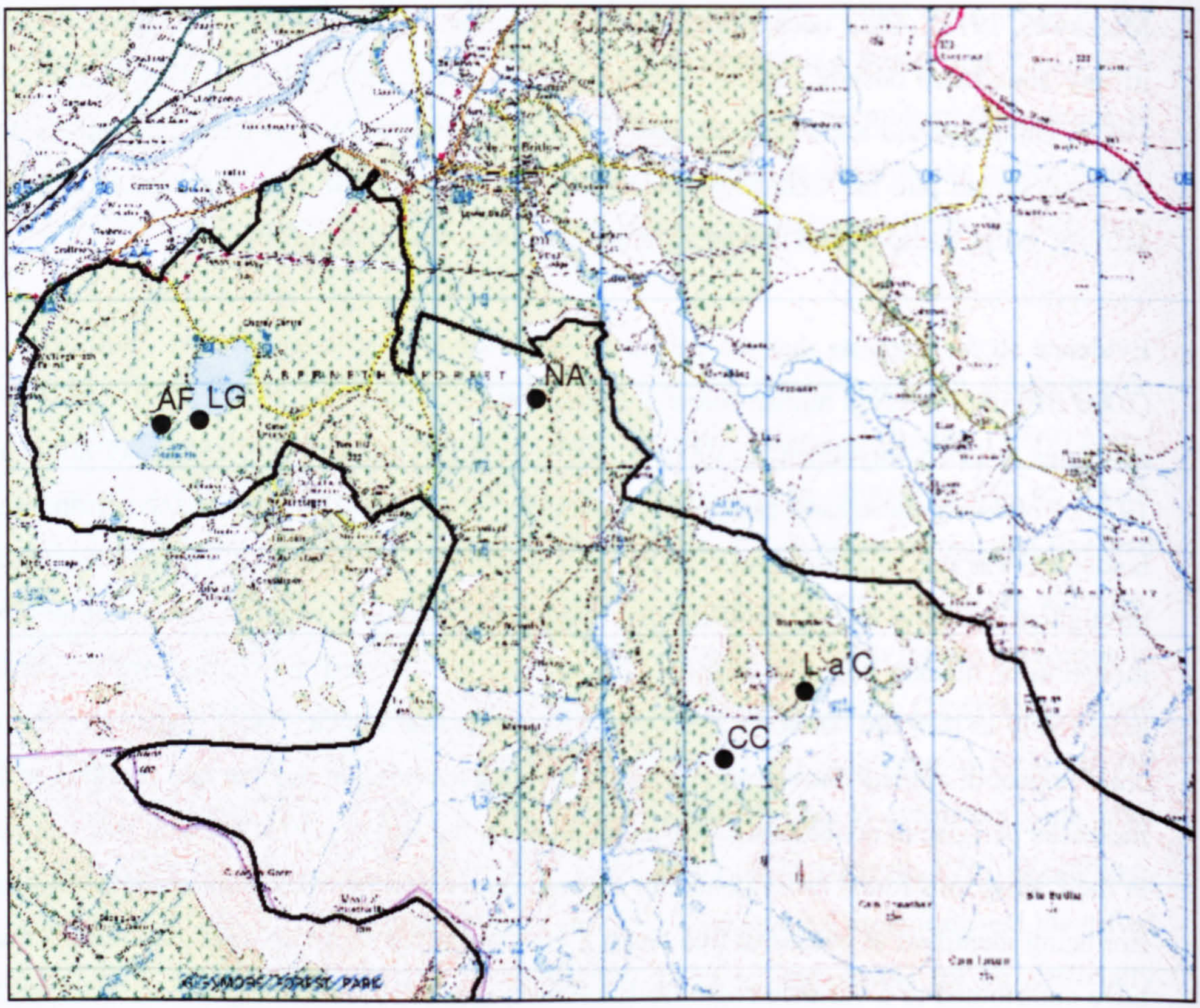


Fig. 5.1. Location of regional cores from Abernethy Forest: AF = Abernethy Forest (Birks and Mathewes, 1978); LG = Loch Garten (O'Sullivan, 1974a); L a'C = Loch a'Chnuic (O'Sullivan, 1974a); NA = North Abernethy (this chapter); CC = Carn a'Chnuic (this chapter).

Previous regional palaeoecological records from Abernethy Forest

Incorporating around 15% of the remaining semi-natural pine forest (Summers *et al.*, 1997), Abernethy nature reserve has been the subject of much research over the past forty years or so, including several classic examples of complete, or near complete, regional Holocene sequences which date from the 1970s (Abernethy Forest: Birks, 1970; Birks and Mathewes,

1978; Loch Garten, Loch a'Chnuic: O'Sullivan, 1974a, 1977; see Fig. 5.1). These are reviewed by Gordon (1993) and Bennett (1996) and are summarised here. Birks (1970) used pollen, sediment stratigraphy and macrofossils to describe a full Holocene sequence from a channel bog between Loch Mallachie and Loch Garten (Fig 5.1). From this hydroseral succession from open water to reed swamp through to bog with *Pinus*, six local 'Abernethy Forest Pollen' zones (AFP1-AFP6) were identified from which five regional pollen zones were defined (Fig. 5.2).

A second core was taken from nearby Loch Garten by Birks and Mathewes (1978), which is regarded as the principal late-glacial sequence for the Cairngorms area (Bennett, 1996; Figs. 5.1 and 5.2). In this profile, local zones AFP1 to AFP3 were radiocarbon dated to *c.* 14,000 – 11,000 cal. BP (12,100 -9700 BP), *i.e.* late Devensian in origin (Birks and Mathewes, 1978), and together correspond with the regional Gramineae (*sic*)-*Rumex-Artemisia* zone described in Birks (1970). With a low pollen influx and dominance of species favouring open conditions, this represents the colonisation of de-glaciated moraine by pioneer grass/sedge communities.

AFP4 (*c.* 11,000-9700 cal. BP; 9700-8700 BP) corresponds to the *Betula-Juniperus communis* zone of Birks (1970; Fig. 5.2) and marks the beginning of the Holocene. Trees and shrubs became dominant over herbaceous species, followed by progressive development of *Betula* woodland, with *Corylus/Myrica* pollen arriving later (Birks, 1970). AFP5 (*c.* 9700-8100 cal. BP; 8700-7200 BP) corresponds to the *Betula-Corylus/Myrica* zone of Birks (1970), and is interpreted as a birch forest colonised by hazel, which was believed to have been a widespread forest type across northern and western Britain at this time (Birks, 1970; Birks and Mathewes, 1978). From the paucity of herb taxa from non-lake margin habitats, this was inferred to be quite dense forest. AFP6 (*c.* 8100-6400 cal. BP; 7200-5500 BP) was the top section of the Birks and Mathewes (1978) profile, and from pollen and macrofossil evidence it was deduced that *Pinus* arrived in the area *c.* 8100 cal. BP (7200 BP), reaching the vicinity of Loch Garten by 7700 cal. BP (6800 BP). It was concluded that *Betula* remained abundant, but *Corylus* declined,

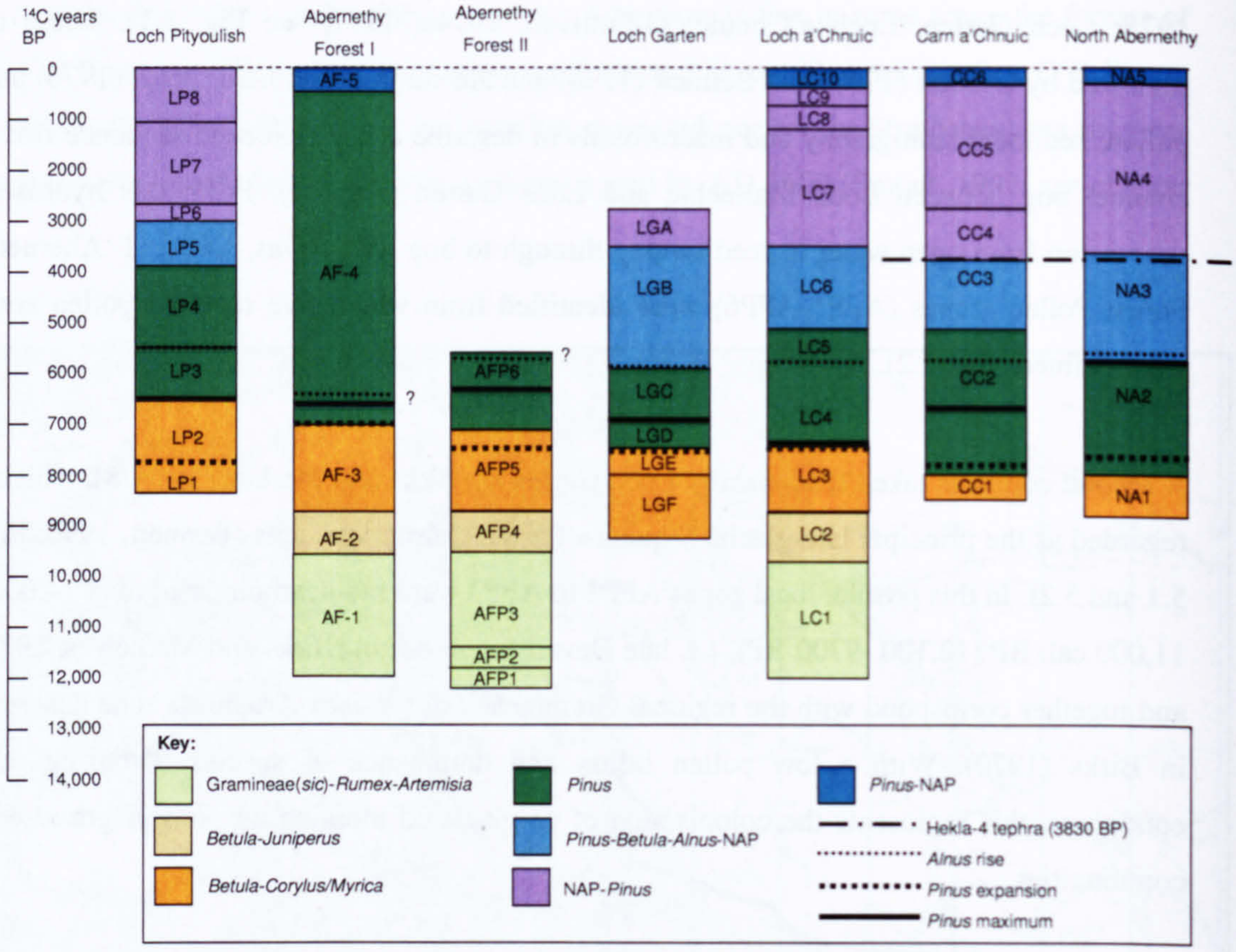


Fig. 5.2. Suggested correlation between previously published pollen assemblage zones for the Abernethy Forest area and the Carn a'Chnuic and North Abernethy profiles. Age estimates are in uncalibrated radiocarbon years BP (see text for calibrated ages). For the Abernethy Forest I profile, the question mark denotes uncertainty relating to the integrity of the sediment profile, whereas in Abernethy Forest II the core may be truncated before the *Alnus* rise is completed. Sources: Loch Pityoulish: O'Sullivan, 1976; Abernethy Forest I: Birks, 1970; Abernethy Forest II: Birks and Mathewes, 1978; Loch Garten and Loch a'Chnuic: O'Sullivan, 1974a.

presumably because of its intolerance to increasingly acid conditions as bog vegetation developed.

O'Sullivan (1974a) examined two sequences from the Abernethy Forest area, a peat sequence from the margins of Loch a'Chnuic and a shallow water lake core from Loch Garten (Figs. 5.1 and 5.2). Although the Loch Garten sequence was an incomplete Holocene record, radiocarbon age estimates were obtained for the *Pinus/Betula* pollen assemblage preceding the rise in *Pinus* pollen (*c.* 8400 cal. BP; 7600 BP), the rise in percentage *Alnus* pollen from <1% to 4% (*c.* 6700 cal. BP; 5900 BP) and a rise in percentage non-arboreal pollen (NAP) (*c.* 3900 cal. BP; 3600 BP). The date for the start of rise in percentage *Pinus* pollen matches well with that of Birks and Mathewes' (1978) core from Loch Garten (*c.*

8400 cal. BP; 7500 BP), if their age-depth model is used to date corresponding points of the pollen record.

O'Sullivan (1974a) noted a decrease in the proportion of *Pinus* pollen and an increase in the proportion of pollen from heathland taxa such as *Calluna*, *Juniperus* and Poaceae *c.* 3900 cal. BP (3600 BP). This was interpreted as the beginning of local, temporary forest clearances around the lake, and was linked to a population influx into Speyside, possibly associated with the construction of local examples of Clava-type chambered tombs which have been dated to this period on the basis of archaeological evidence (O'Sullivan, 1974b). From similar fluctuations in the earlier pollen record he suggested such clearances may have started as early as 6100 cal. BP (5400 BP). O'Sullivan (1974a) suggests that this phase of more local, temporary clearances continued until *c.* 1500 cal. BP to 1000 cal. BP (1500-1000 BP), when a second phase of more extensive, permanent clearances began, marking the beginning of major heathland formation at Abernethy. This was linked with evidence for late Iron Age/early medieval settlement and a nearby Iron Age fort at Avielochan. However, as Loch Garten is a relatively large lake, the pollen signal is likely to reflect a large pollen source area, so clearances may not necessarily have been confined to the area around the loch itself. Further studies of palaeoecological records from a network of smaller sites around the reserve are needed to allow better assessment of the timing and spatial extent of forest clearance in the area.

O'Sullivan (1974a) used pollen and historical evidence to suggest that the area west of Loch Garten was not forested in the mid-eighteenth century prior to replanting from A.D.1840. This contrasts with the area around Loch a'Chnuic, where he suggests that the forest was little disturbed until the last 200 years, except for gradual increase in percentage *Calluna* pollen that may indicate opening of canopy to grazing (O'Sullivan, 1977). O'Sullivan's (1973a) work on recent heathland-forest transitions at Abernethy from *c.* 1500 cal. BP (1500 BP) to the present is reviewed in chapter 6, which focuses on the last 5000 years.

Since the above studies were published, there has been little work on the long term dynamics of this region other than a study of the *Pinus sylvestris* tree line (McConnell and Legg, 1995; McConnell, 1996) and an assessment of the status of wooded bogs at Abernethy Forest (McHaffie *et al.*, 1999; 2002; Legg *et al.*, 2003). The palaeoecological studies carried out in Abernethy Forest during the 1970s are mainly based on sediments from lakes or large bogs, which has resulted in a bias towards a regional pollen signal (*sensu* Sugita, 1994). This

makes it difficult to determine local variations in vegetation development, as human activity tends to be unevenly distributed in the landscape, and operates at a smaller scale than can be detected by regional pollen records (Birks, 1986).

The long term fire history at Abernethy nature reserve has not been widely studied, with several recent studies focusing only on the recent past at a local scale (Cavalho, 1999; McHaffie *et al.*, 1999; chapter 2). Consequently, little is understood about fire regimes and their effects on the origins and development of vegetation. Further studies, incorporating both regional and local charcoal records, are needed to learn more about the major processes that have led to the landscape mosaic that exists today, particularly in relation to the combined effects of fire and other human activity. These factors are likely to have affected not only the development of heathland but also the diversity of the forest. Forest composition is thought to have been more varied in the past, having become less so largely as a result of human interference (O'Sullivan, 1977).

In this chapter, pollen, charcoal, *Pinus* stomata and peat stratigraphical records are interpreted for two sites, using correlations between both sequences and other regional profiles for the area to identify regional events. Full details of the rationale for selecting these methods are given in chapter 2. Macroscopic and microscopic charcoal records were used to infer regional and local fire history, and *Pinus* stomata to infer local presence of *Pinus*. This information is useful when attempting to interpret sequences from bog sediments, as unlike lakes, the pollen record contains a local component from plants growing on the bog surface and a regional component from plants growing far away. Local presence of Pinus can therefore be used to pinpoint periods when the pollen record was reflecting local vegetation to a greater degree relative to the regional vegetation, bearing in mind that the absence of stomata is not necessarily an indicator of the absence of local Pinus. An isochronous horizon for 4260 cal. BP (3830 BP) is identified using the Hekla-4 tephra, which provides a marker for comparing the sequences with existing profiles from the reserve. Differences between the profiles are used to detect changes in the scale at which the basin reflected the surrounding vegetation. From these studies, a new synthesis of long term vegetation history is produced.

Study area

A full description of Abernethy nature reserve and the 15 km x 15 km study area is given in chapter 1.

Site selection

Despite the potential problems of changes in opening size, and consequently, pollen source area over time, bogs were selected for study rather than lakes on the basis that pollen and charcoal landing on a bog surface is less likely to be disturbed than that accumulating in lake sediments. It was hoped that any differences between the way in which lakes and large bogs for this region recorded the surrounding vegetation would be apparent from comparison of pollen records across all profiles. It was considered likely that the effects of major changes in opening size on the pollen signal would be reduced by using sites within well-defined topographical basins. Sites were selected from large basins which had no trees or sparse, often stunted tree growth at the centres, with well-defined margins between the bog surface and the surrounding vegetation.

Methods

Field methods

Two large basins with deep peat (>3 m) within the main forested area of Abernethy were selected with the intention of obtaining pollen records at the regional scale. Cores were extracted from deeper, apparently undisturbed parts of each basin using a 5 cm diameter x 1 m long Russian sampler. Peat stratigraphy for each section was logged in the field using the Troels-Smith (1955) sediment description system and later confirmed in the laboratory. The sections were securely wrapped and refrigerated until required.

The first core was taken from a large bog at North Abernethy (NA), National Grid Reference NH 012178 (Fig. 5.1). At present the bog is surrounded by pine forest, thinning into scattered, stunted trees which are present across much of the bog surface. The core was taken from apparently uncut deep peat within an area of low tree density in the northern part of the bog. The second core, Carn a'Chnuic (CC), was taken around 5 km further south (National Grid Reference NH 035 136), from the centre of a treeless bog *c.* 300 m x 300 m, around 1 km south of the Carn a'Chnuic summit (Fig. 5.1). The basin lies within a fairly open part of the forest within a *c.* 1 km wide pass through which the Crom Allt stream flows from Loch a'Chnuic to the river Nethy.

Laboratory methods

Tephra

Tephra geochemistry was determined at the Tephrochronological Analytical Unit at the University of Edinburgh, as described in chapter 2.

Charcoal

Microscopic charcoal area was estimated using Clark's (1982) point count method, and the charcoal to pollen ratio calculated (referred to hereafter as the C:P index; see chapter 2). Macroscopic charcoal was prepared by wet sieving, and the concentrations presented are for the 150 to 250 μm size class. For macroscopic charcoal, concentrations above 50 particles per cm^3 in the selected size class were defined as local fires (see chapter 2; Whitlock and Larsen, 2001).

Pollen and stomata

Samples for pollen and stomata were prepared using standard techniques (Moore *et al.*, 1991) as described in chapter 2 and pollen was counted to at least 200 ± 50 Total Land Pollen (TLP). It was not possible to differentiate *Corylus avellana* pollen from that of *Myrica gale* (see Edwards, 1981) so the term *Corylus*-type was used to include both taxa. Zonation of pollen diagrams was carried out in *psimpoll v.4.10* (Bennett, 2002) using the constrained incremental sum of squares method; for ease of discussion the dissimilarity cut-off levels for each zone were selected subjectively.

Results

Tephra

Using light microscopy, one tephra layer was located in NA (peak shard concentration 96-98 cm), and two in CC. The upper layer in CC shows evidence of upward and downward shard dispersal but peak shard concentration occurred between 142 cm and 146 cm. There was no determinable peak for shards between 288 cm and 435 cm (see Fig. 7.1., chapter 7). At least ten shards were analysed for each tephra and full details of shard composition are given in Appendix 1a. The lower layer in CC was not characterised, as its extreme vertical spread made it unsuitable for use as a marker horizon.

For identification purposes, the percentages of calcium and magnesium oxides are plotted against those of representative shards of known reference tephras as published by Dugmore *et al.* (1995). Fig. 5.3 shows that the tephra studied falls within the representative composition of Hekla-4 (*c.* 4260 cal. BP) at both sites. The isochrone was therefore identified at 96 cm to 98 cm for North Abernethy sequence and tentatively at 142cm to 146 cm for Carn a'Chnuic.

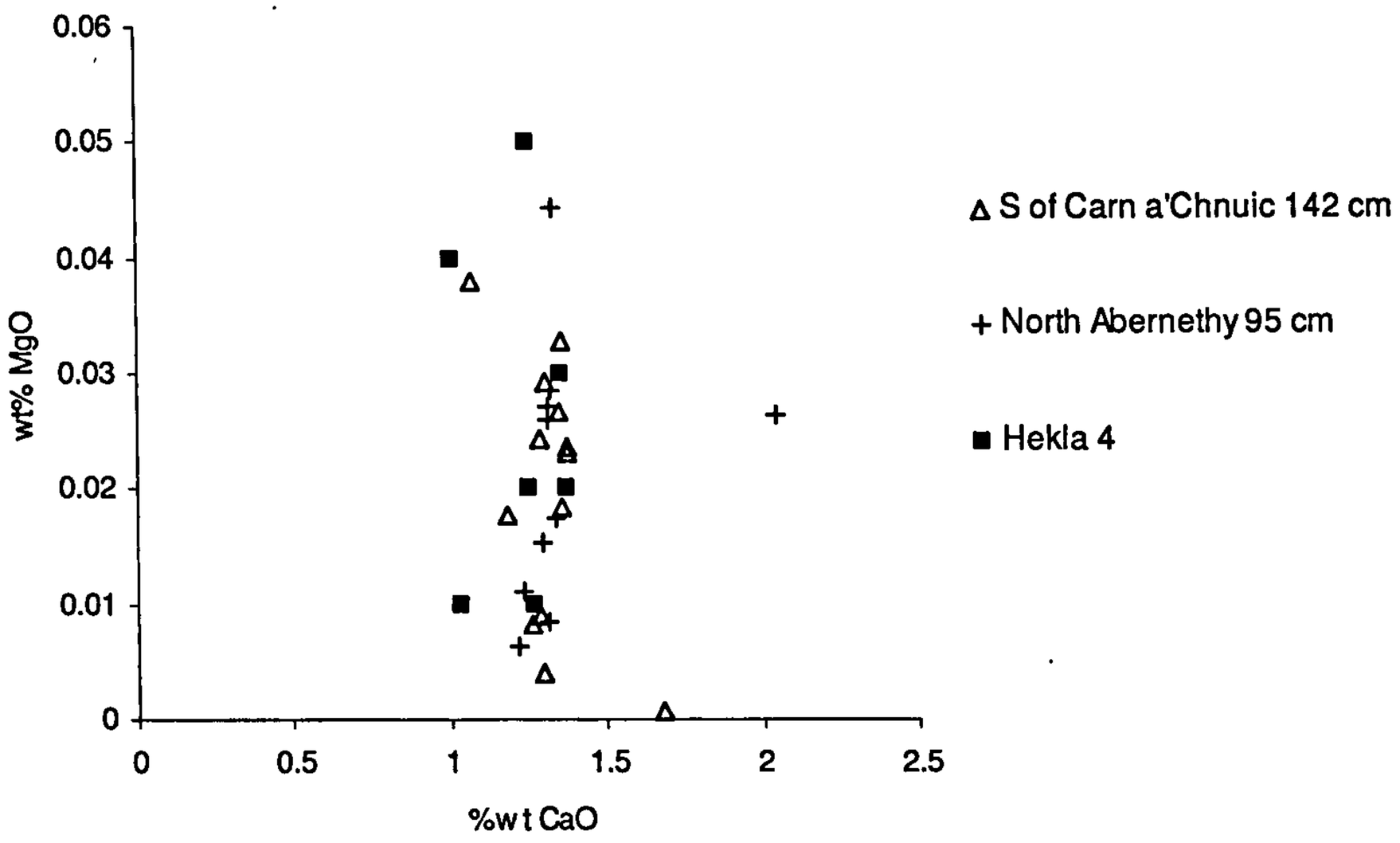


Fig 5.3. Relationship between calcium and magnesium oxides for tephra layers in two profiles from Abernethy Forest plotted with Dugmore *et al.* 's (1995) representative analyses of the Hekla-4 tephra.

Chronology

Pending the outcome of an application for radiocarbon dating, the timing of significant events is estimated by comparison with previously published estimates based on radiocarbon dated cores from Loch Pityoulish (O'Sullivan, 1976), Abernethy Forest (Birks and Mathewes, 1978) and Loch Garten, (O'Sullivan, 1974a). Tentative biostratigraphic correlations were also made with cores from Abernethy Forest (Birks, 1970) and Loch a'Chnuic (O'Sullivan, 1974a). These are shown in Fig. 5.2.

In addition, the Hekla-4 tephra isochrone provides a useful chronological marker, occurring in both cores near the top of the *Pinus-Betula-Alnus* zone, supporting the idea that both sequences recorded the vegetation at a regional scale. However, the dispersed nature of tephra at CC suggests that some form of disturbance has affected the tephra shards. Shards may be more likely to undergo downward movement than pollen on account of their greater specific gravity. Such disturbance may have been related to the presence of tree roots, which may have disturbed the sediment during or after growth, or it may have been related to other forms of internal channelling and/or water movement (see Payne *et al.*, 2005). Since the pollen record from CC shows similar trends to those of NA and other regional profiles from the area, pollen may not have been as disturbed as the tephra. Hence this core is included in the analysis, but the results are interpreted with caution.

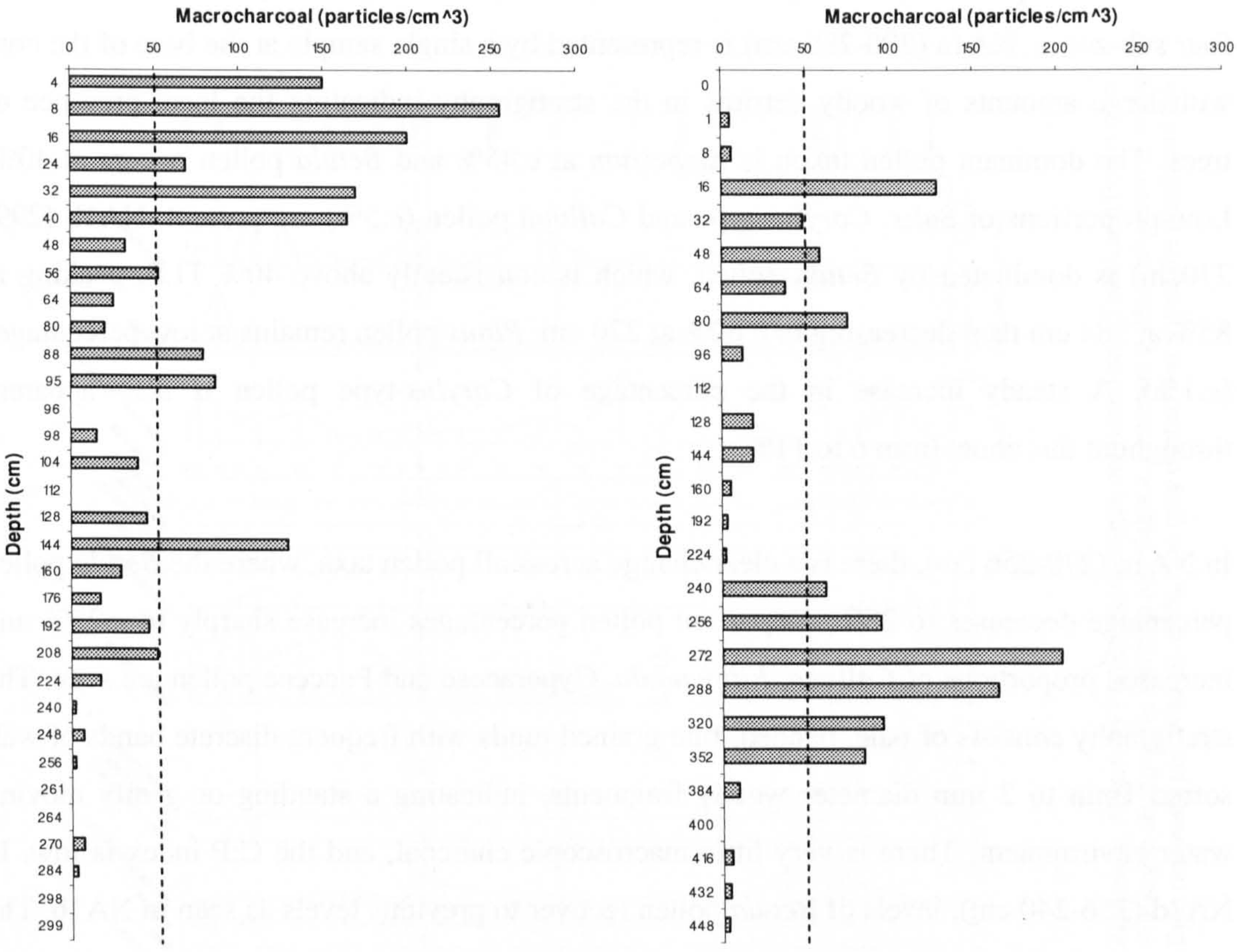
Stratigraphy

Site NA was cored to 300 cm, where firm resistance was met; the presence of large amounts of woody detritus in the lower 30 cm of the sequence suggests that this is due to the presence of a woody layer. The sediment recovered is mainly well-humified *Eriophorum* peat, with a sharp transition to a zone of fine muds between 250 and 270 cm. The lower 60 cm of the sequence contains frequent woody detritus within the matrix; this is largely absent above 240 cm. Above 60 cm the sedge peat is much less humified and contains *in situ* rootlets and *Eriophorum* remains.

Site CC was cored to an impenetrable layer at 435 cm. No mineral or woody detritus was apparent in the basal sediments, which comprise well humified *Eriophorum* peat to a depth of 360 cm, becoming gradually less humified to 155 cm, at which point the degree of humification increases. There is little change until 45 cm, other than a layer of darker, highly saturated peat between 93 and 100 cm. From 45 cm to the top of the profile, poorly humified *Eriophorum* peat is observed with *in-situ* leaves and roots. A 250 cm long *Pinus* root was retrieved with the 250 to 350 cm section, but this was outside the chamber so its stratigraphic position is unknown. Frequent macroscopic charcoal flecks occur between 240 and 270 cm.

Charcoal analysis

Microscopic and macroscopic charcoal records are shown in Figs. 5.5a and 5.5b, and macroscopic charcoal counts are also shown in Fig. 5.4 to indicate possible local fire events. In both profiles there are two major cycles of increase in both microscopic and macroscopic charcoal, with a period in both records where microscopic charcoal is low or virtually absent. In the top 20 cm of the profiles, macroscopic charcoal reaches its maximum abundance at NA, whereas at CC levels have decreased.



a) b)

Fig 5.4. Macroscopic charcoal counts for North Abernethy (a) and Carn a'Chnuic (b). The dotted line shows the cut-off level above which local fire events are indicated, which was defined as >50 particles per cm^3 (after Whitlock and Larsen, 2001).

Pollen analysis

Summary pollen diagrams are shown as Fig. 5.5a and 5.5b (for full diagrams, see Appendix 2a). Pollen percentages are rounded to the nearest 5% or nearest 1% for levels <5% TLP. Five local pollen assemblage zones were defined for NA and six for CC, which are referred to as NA1-NA5 (North Abernethy) and CC1-CC6 (Carn a'Chnuic).

Zone descriptions

Zone assemblages have features in common across both cores (Fig. 5.2). For explanation of humification index scores see chapter 2, Table 2.2.

North Abernethy

NA1 (300-245 cm)*: Betula-Corylus-type* zone

This zone comprises well-humified sediment (humification index = 3) and is divided into four sub-zones. NA1a (300-299 cm) is represented by a single sample at the base of the core with large amounts of woody detritus in the stratigraphy indicating the local presence of trees. The dominant pollen taxon is *Empetrum* at *c.*45% and *Betula* pollen occurs at 40%. Low proportions of *Salix*, *Corylus*-type and *Calluna* pollen (*c.*5%) are present. NA1b (299-270cm) is dominated by *Betula* pollen, which is consistently above 40% TLP, peaking at 85% at 284 cm then decreasing to *c.*60% at 270 cm. *Pinus* pollen remains at low percentages (*c.*1%). A steady increase in the percentage of *Corylus*-type pollen is also apparent throughout this zone, from 6 to 11%.

In NA1c (270-256 cm), there is a clear change across all pollen taxa, where the *Betula* pollen percentage decreases to 25%, *Empetrum* pollen percentages increase sharply to *c.*25% and increased proportions of *Calluna, Filipendula*, Cyperaceae and Poaceae pollen are seen. The stratigraphy consists of pale, banded, fine grained muds with frequent discrete bands of well sorted 1mm to 2 mm diameter woody fragments, indicating a standing or gently moving water environment. There is very little macroscopic charcoal, and the C:P index is low. In NA1d (256-240 cm), levels of *Betula* pollen recover to previous levels as seen in NA1b. The percentages of *Corylus*-type pollen remains relatively high at >20%, and *Calluna* and *Empetrum* pollen are both present at levels of *c.*8%. The C:P index is extremely low in this zone and there is no indication from the macroscopic charcoal of any local fires having occurred. No *Pinus* needles or stomata are observed in this zone.

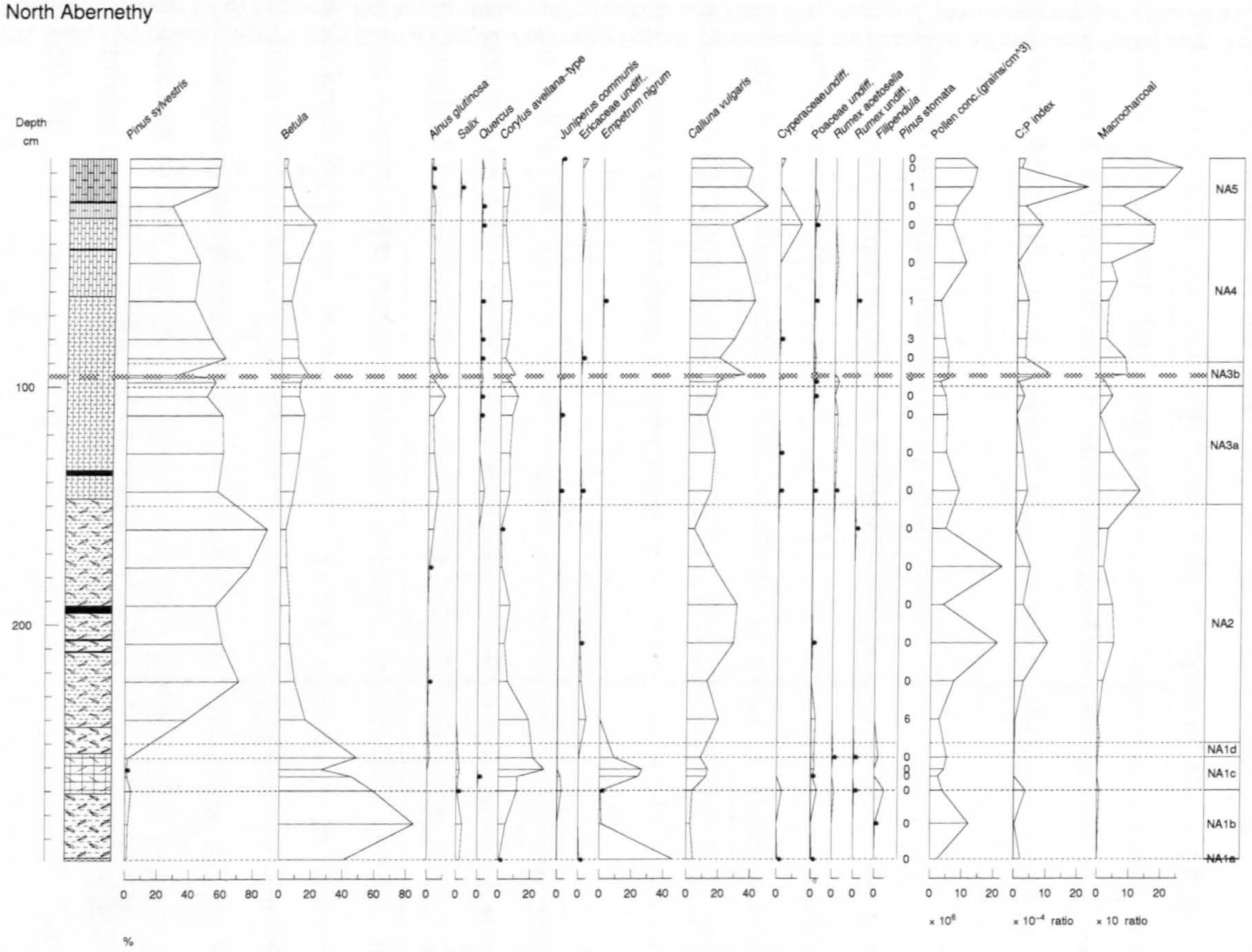


Fig. 5.5a. Summary pollen diagram from North Abernethy, Abernethy Forest. Percentages are based on a Total Land Pollen sum (Total Land Pollen and Spores for *Sphagnum*). For key to stratigraphic symbols see Table 2.1, chapter 2. Macrocharcoal is measured as particles cm^{-3} in the 150-250 µm size class. Dots represent percentages < 1%. The grey dashed line shows the position of the Hekla-4 tephra deposit.

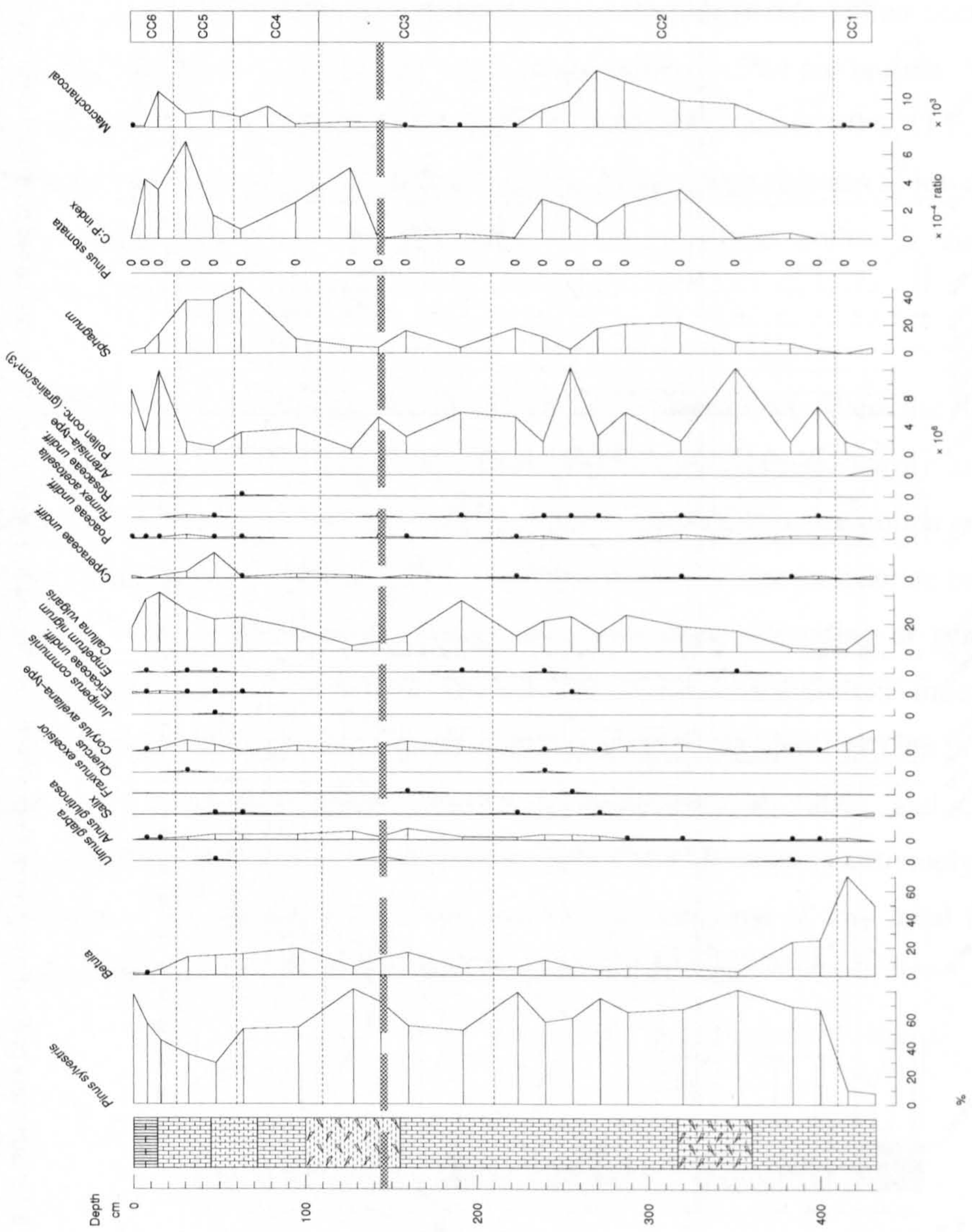


Fig. 5.5b. Summary pollen diagram from Carn a'Chnuic, Abernethy Forest. Percentages are based on a Total Land Pollen sum (Total Land Pollen and Spores for *Sphagnum*). For key to stratigraphic symbols see Table 2.1, chapter 2. Macrocharcoal is measured as particles cm^{-3} in the 150-250 µm size class The grey dashed line shows the position of the Hekla-4 tephra deposit.

NA2 (240-150 cm) *Pinus* zone

In NA2 the dominant pollen type is *Pinus*, with levels rising from *c.*40% at the beginning of the zone to *c.* 50-60%, with peaks of 70% at 224 cm and *c.*90% at 160 cm. *Corylus*-type

pollen percentages decrease from *c.* 20% to *c.* 5%. A single *Alnus* grain was seen at 224 cm, then from 176 cm *Alnus* pollen appears consistently, occurring in all samples from this point and rising from <1% to levels of *c.*5-10% by 140 cm. There is a decrease in *Betula* pollen from *c.*15% at the base of the zone (240 cm) to a fairly consistent level of <5% for the remainder of the zone. The sediment is generally well humified (humification index = 3), with *Eriophorum* fragments detectable under a stereomicroscope, although in the basal 2 cm the peat is springy, lighter in colour with visible rootlets (humification index = 2). Six *Pinus* stomata are present in the basal sample of this zone but no *Pinus* needles are observed.

NA3 (150 - 90 cm): *Pinus-Betula-Alnus* -NAP zone

This zone is divided into two pollen sub-zones. At the base of NA3a (150-98 cm), *Betula* pollen percentages increase gradually to *c.* 10-15%. Both *Alnus* and *Corylus*-type pollen percentages increase from *c.*5% to 10%, whilst *Pinus* pollen percentages decrease slightly. An increase in the frequency of NAP taxa, in particular, heathland taxa such as *Calluna*, Poaceae, Cyperaceae and *Rumex* is observed.

Sub-zone NA3b (98 -95 cm) shows a series of marked changes in the proportions of all major pollen taxa, pollen concentration and charcoal values. No change in stratigraphy from partly-humified *Eriophorum* peat was observed (humification index = 2). At 96 cm, both *Alnus* and *Corylus*-type pollen proportions decrease from *c.*10% to *c.*2%, but recover to previous levels by 95 cm. At 95 cm, there is a sharp decrease in the percentage of *Pinus* pollen from *c.*55% to 30% (95 cm), followed by recovery to 60% by 88 cm. This is reflected by the changes in percentage *Calluna* pollen, which increases from 20% to 35% at 95 cm, then decreases to 20% by 88 cm. *Betula* pollen percentages also increase slightly. Peak concentrations of tephra identified as being from the Hekla-4 eruption date this sub-zone to *c.*4260 cal. BP.

NA4 (90-30 cm): NAP zone

NA4 is marked by a return to previous percentages for most major pollen taxa. *Pinus* pollen declines from 70% to 55% by the end of the zone, although other tree taxa are present in relatively stable proportions. The increases in *Calluna* pollen seen in NA3a continue, peaking at 40% then decreasing to 25% at the top of the zone. *Quercus* pollen occurs more frequently, but at low levels (<1%). Small numbers of *Pinus* stomata are present in the lower part of the zone but no needles are observed. The sediment remains partly humified

Eriophorum peat (humification index = 2). Ericaceae *undiff.* pollen is occasionally present at low levels of 1%. There is a peak of Cyperaceae pollen (>10%) at 32 cm, the first time since the base of the sequence that it has been present at levels >1%. The onset of a sustained increase in macroscopic charcoal abundance is observed in this zone.

NA5 (30-0 cm) NAP-*Pinus* zone

This zone is defined by a reverse in the decline of *Pinus* pollen which increases from *c.*25% to stabilise at around 55% within the top 20 cm of the profile. The sediment is well-preserved *Eriophorum* peat (humification index = 1).There is a consistently high concentration of both microscopic and macroscopic charcoal in this zone, including the highest concentration of macroscopic charcoal sampled from the entire profile at 8 cm.

Carn a'Chnuic

CC1 (435 - 410 cm) *Betula-Corylus*-type zone

This zone comprises partly decayed, dry sedge peat (humification index = 2), with *in-situ* Eriophorum remains. *Betula* is the dominant pollen, increasing from 50% to *c.*70%. *Pinus* pollen percentages are low (*c.*10%) at this time and percentage *Calluna* pollen shows a decrease from *c.* 15% to 2%. The onset of a rapid decline in the percentage of *Corylus*-type pollen from 16% to 8% was observed. *Artemisia*-type pollen (4%) occurs in the basal sample of the core at 432 cm. Charcoal values are low.

CC2 (410 – 210 cm) *Pinus* zone

In this zone, the sediment is also partly decayed *Eriophorum* peat (humification index = 2), slightly wetter than in CC1. The percentage of *Pinus* increases rapidly to *c.* 70% at 400 cm then *c.*80% by 352 cm. At 384 cm, the onset of a gradual increase in percentage *Calluna* pollen was observed, increasing from <5% to levels of around 20-25% by 320 cm. The percentage of *Calluna* pollen correlates significantly with the C:P index ($r = 0.75$, $p < 0.01$, $n = 9$) and macroscopic charcoal abundance ($r = 0.60$, $p < 0.05$, $n = 9$), the latter occurring at levels well above that selected to indicate local fire events. *Alnus* occurs at consistently higher levels (*c.* 3-10%) from 272 cm. The *Corylus*-type pollen percentage decrease first seen in CC1 continues, with *Corylus*-type pollen decreasing to 1% at the start of this zone, only recovering slightly to levels below <5% throughout the remainder of the zone. The proportion of Poaceae pollen remains low (<1%).

CC3 (210-110 cm) *Pinus-Betula-Alnus-NAP* zone

Between 210 cm and 155 cm, the sediment comprises well-preserved *Eriophorum* peat (humification index = 1), but is more humified between 155 and 110 cm (humification index = 2).The base of this zone is marked by a decrease in percentage AP, initially reflected by a decrease in *Pinus* pollen percentages to *c.*50% at 192 cm. The recovery in AP at 160 cm is not related to *Pinus* pollen percentages, which remain at *c.* 50%, but to an increase in *Betula*, *Alnus* and *Corylus*-type pollen percentages, which together comprise 30% of TLP. The decrease in AP at 192 cm is mirrored by an increase in *Calluna* pollen percentages, but at 160 cm there is the onset of a decline in percentage *Calluna* pollen, which falls to <5% by 128 cm. The region of peak Hekla-4 tephra concentration was observed around this depth, which coincides with a peak in percentage *Pinus* pollen of *c.*80%, giving this part of the profile an estimated date of *c.*4260 cal. BP. Levels of both microscopic and macroscopic charcoal show a marked decrease from the previous zone, although there is a large peak of microscopic charcoal at 128 cm. Levels of macroscopic charcoal remain well below the level selected to indicate local fire events.

CC4 (110-60 cm) NAP-*Pinus* zone

Sediment is *Eriophorum* peat similar to that of CC3, becoming darker in colour and more humified above 93 cm (humification index = 2). A steady increase in percentage *Calluna* pollen is seen, to 30% by the top of the zone. *Pinus* pollen remains dominant but shows quite a sharp decrease from 55% to 35%. *Betula* pollen percentages fluctuate less than in zone CC3, staying at around 15%. There is little change in the proportion of *Alnus* and *Corylus*-type pollen, both occurring at levels of *c.*5%. The microscopic charcoal signal is high but variable, whilst macroscopic charcoal occurs at consistently higher levels than in CC3.

CC5 (60-25 cm) NAP zone

Sediment comprises *Eriophorum* peat similar to that of CC4, becoming gradually less humified above 45 cm (humification index = 1).The start of this zone is marked by the decrease in percentage *Pinus* pollen to *c.*30%, increasing to *c.*35% at 32 cm. *Alnus* is present at levels of c. 4% and *Corylus*-type pollen percentages decrease from 10% to 5%. There is an increase in the proportion of NAP pollen taxa, with the proportion of *Calluna* pollen continuing to increase steadily to *c.* 40%, and a marked increase in the proportion of Cyperaceae pollen, reaching a value of *c.* 20% at 48 cm. High levels of microscopic and macroscopic charcoal are present in all samples, at levels that frequently satisfy the criterion for local fire events.

CC6 (25-0cm) *Pinus-NAP* zone

This zone comprises partly humified *Eriophorum* peat (humification index = 1), with *in situ* roots and leaves clearly visible. There is an increase in *Pinus* pollen from 35% to >75%, with a corresponding decrease in percentage *Calluna* pollen. In the top 10 cm of the profile, *Betula* pollen has all but disappeared from the pollen record, occurring at levels of 1%. *Alnus* and *Corylus*-type pollen percentages are c. 1% at 8 cm and not seen in the top surface sample. There is also a decline in microscopic and macroscopic charcoal in this zone.

Site development history

North Abernethy

Vegetation history

The high percentage value for *Empetrum* pollen at the base of the profile may indicate relatively dry conditions prior to peat accumulation (Tallis, 1997) and the presence of a widespread timber layer and woody detritus at the base of the recovered sediment indicates that this basin once supported trees. On the basis of the pollen record and the frequent occurrence of distinctive bark fragments it is concluded that these were *Betula*. The well-humified basal deposits of zone NA1 suggest that the rate of sediment accumulation was initially low, although the sedimentary environment appears to have been interrupted, indicated by a change in the stratigraphy to banded muds, which indicate the presence of standing or gently moving water. The pollen assemblage during this sub-zone suggests a fen community, with *Corylus*-type pollen interpreted as *Myrica gale* rather than *Corylus*, co-existing with *Salix*, *Filipendula*, Poaceae, Cyperaceae and *Rumex*. Charcoal evidence prior to the rise in percentage *Pinus* pollen suggests that both local and regional fire events were uncommon at this time, which is consistent with a period of higher water tables and increased wetness. From the regional correlation (Fig. 5.2) it can be estimated that this occurred sometime prior to c. 8900 cal. BP (8000 BP).

The less humified sedge peat first seen at the base of zone NA2 indicates that basin infilling was underway by this time, and conditions within the basin were again suitable for trees, although by now *Pinus* had arrived in the area and appears to have been the dominant taxon. Its local presence in the basin is indicated by the presence of *Pinus* stomata. *Calluna* was probably locally present on the bog surface, as its pollen proportion fluctuates with changes in the abundance of macroscopic charcoal. The latter is consistently present and occasionally indicative of local fire events throughout most of zones NA2 and NA3. *Alnus* pollen is first recorded in zone NA2 at around the time of the increase in percentage *Pinus* pollen. Zone

NA2 may reflect dominance of the surrounding area by *Pinus* forest, as there is no indication from the stratigraphy that *Pinus* was present locally (*i.e.* no stomata or wood macrofossils are seen). The first consistent presence of *Alnus* is at 176 cm, suggestive of restricted but more local presence.

In zone NA3 (estimated age range 6800 cal. BP (6000 BP) to 4260 cal. BP (3830 BP); Fig. 5.2), the proportion of *Betula* relative to *Pinus* increases (mean *Pinus* to *Betula* ratio for NA2 = 12; for NA3 = 4), suggesting that *Betula* was a more significant component of the surrounding forest than previously. The relative proportions of *Alnus* and *Corylus*-type pollen also increase. This may relate to the beginnings of temporary clearances, as changes in the charcoal record strongly suggest human activity had begun around this time (see below). Disturbance may have remained at a level that allowed the colonisation of broad-leaved species that favour gaps in the canopy (*cf.* Tipping *et al.*, 1999).

In zone NA4 (c. 4260 cal. BP- 300 cal. BP; Fig. 5.2) the decrease in the proportion of *Calluna* pollen may be related to increased local fire events on the bog surface, with loss of *Calluna* temporarily reducing the local component of the pollen signal. If this was the case, it appears that the surrounding forest remained a mix of *Pinus* and *Betula* with smaller amounts of *Corylus*-type and *Alnus*. The decline in percentage *Pinus* pollen relative to *Betula* suggests a reduction in *Pinus* forest. The increase in percentage *Calluna*, corresponding with an increase in macroscopic charcoal abundance, may be related to its increased local presence but there is no direct evidence for this.

The increase in *Pinus* pollen percentages near the top of the core in zone NA5 probably represents planting of *Pinus* over the past *c.* 300 years. The near-absence of *Betula* pollen suggests this species was, and remains, much depleted in the forest since planting began. The presence of *Pinus* stomata indicates that there were trees present on the bog. The pollen record appears to have changed little in the top 20 cm of the core, suggesting that there has been relatively little change in the bog or surrounding vegetation since the period of increased *Pinus* planting.

Fire history

The similarity of the macroscopic charcoal record and C:P index for the North Abernethy sequence (Figs. 5.3, 5.5a) suggest that the microscopic charcoal signal is dominated by local rather than regional charcoal. Little charcoal is seen in zone NA1, but both macroscopic and

microscopic charcoal are estimated to increase *c.* 7500 cal. BP (6500 BP) to a consistent presence throughout the remainder of the sequence. Levels fluctuate throughout zones NA2-NA4 but the biggest change occurs midway through zone NA4, where macroscopic charcoal reaches unprecedented levels. Almost all samples are indicative of local fire events according to Whitlock and Larsen's (2001) criterion. Such a marked change in the charcoal record may reflect human fire activity, with the fire regime intensifying for a second time *c.* 1000 cal. BP (1000 BP; Fig. 5.2). There is a significant correlation between the proportion of *Calluna* pollen and i) macroscopic charcoal abundance (correlation coefficient $r = 0.52$, $p < 0.005$, $n = 28$); ii) microscopic charcoal (as C:P index: $r = 0.38$, $p < 0.025$, $n = 28$). This suggests the pattern of local fire is strongly related to the development of *Calluna* heathland, and whilst humans may have burnt the heathland, it does not necessarily follow that heathland development was in itself due to anthropogenic activity; factors such as climate change may also have been involved. High levels of macroscopic charcoal in zone NA5 may indicate that fires documented in the eighteenth century (see Summers, 2005) affected this site.

Carn a'Chnuic

Vegetation history

At the base of this profile, wood fragments and the dominance of *Betula* in the pollen record suggest that this basin probably once supported birch woodland before becoming too wet for tree growth c. 8900 cal. BP. A fen community then developed as a result of a raised water table, probably associated with wetter climatic conditions. The rapid replacement of *Betula* by *Pinus* as the dominant taxon in the pollen record (CC2) probably reflects a regional scale change as there is no evidence for local tree presence from wood macrofossils or *Pinus* stomata. Subsequent colonisation of the basin by *Pinus* is indicated by the presence of *in situ* *Pinus* roots occurring in the upper section of CC2 and the lower section of CC3, but root penetration prevents stratigraphical inferences from being made.

The sustained high levels of *Pinus* pollen throughout zones CC2 and CC3 suggest that *Pinus* forest remained dominant in the surrounding vegetation from *c.* 8900 cal. BP to *c.* 3800 cal. BP. The fluctuations in percentage *Calluna* pollen may represent local presence related to basin succession, but changes in the composition of the AP signal suggest that the increases in the proportion of *Betula* matched those of *Calluna*, suggesting that more open conditions generally may have been partly responsible for the decrease in percentage *Pinus* pollen.

In zone CC4, a steady increase in percentage *Calluna* pollen occurs alongside an unprecedented decrease in *Pinus* pollen and a similarly unprecedented rise in macroscopic charcoal. This strongly suggests heathland formation in the immediate area which from the location of the tephra appears to have begun shortly after 4260 cal. BP. The uppermost zone, CC5, shows a rapid increase in *Pinus*, probably related to planting in historical times, with associated loss of broadleaved species undesirable in commercial forestry (Taylor, 2000; Summers, 2005)

Fire history

Early on in the record (zone CC1 and the lower section of CC2), during the phase when *Betula* woodland apparently declined as *Pinus* colonised (*c.* 8900 cal. BP), a low abundance of charcoal indicates that regional and local fire events were of minor importance (Figs. 5.3, 5.5b). *In-situ* fire is indicated on the bog surface in zone CC2, which was probably related to the increased presence of *Calluna* although botanical identification of macroscopic charcoal would be required to support this. It seems that once *Pinus* became the dominant taxon (*c.* 8400 cal. BP) and conditions became drier, local and possibly regional fire events were frequent. The increased abundance and continuity of charcoal may reflect human fire activity, suggesting Mesolithic hunter-gatherers were burning this area earlier than previously supposed, possibly as early as *c.* 7500 cal. BP (6500 BP). Trees may have been felled and/or burned locally, as there is a sharp decline in arboreal pollen concentration during this period, but equally this pattern could result from an environmental change to conditions less favourable to trees. Human agency is not unfeasible in the context of O'Sullivan's (1974a) inference that clearances were taking place at nearby Loch a'Chnuic by 6100 cal. BP (5400 BP).

Microscopic and macroscopic charcoal are virtually absent from the record for a second time just prior to the Hekla-4 tephra deposition. As previously, this may be related to a period of increased wetness, although independent proxies would be needed to support this. A further cycle of increased fire events appears to begin just prior to 4260 cal. BP, with the charcoal pattern again suggesting human fire activity. This is compatible with O'Sullivan's (1974a) date for clearances around Loch Garten, but challenges the previous idea that forest near Loch a'Chnuic was largely undisturbed until historic times (O'Sullivan, 1974a). The evidence from this profile suggests that sustained burning of the local basin vegetation was taking place at Carn a'Chnuic from *c.* 3900 cal. BP (3600 BP). There is a close relationship between percentage *Calluna* pollen and charcoal abundance throughout zones CC4 and CC5,

with consistent presence of macroscopic charcoal at levels just below or exceeding the criterion for local fire. A decline in percentage AP is apparent, which suggests that changes in forest cover and fire regime were sufficiently widespread to be recorded in the regional signal, such that a regional climate change cannot be excluded as a causal factor. In the top 10 cm of the profile, the local and regional charcoal signals suggest a marked reduction in fire frequency and/or intensity. Alongside the increase in percentage *Pinus* pollen, this may represent the beginnings of forest planting and fire suppression practices of the mid-nineteenth century onwards.

For the sequence as a whole there is a significant correlation between the proportion of *Calluna* pollen and microscopic charcoal (as C:P index) ($r = 0.42$, $p < 0.025$, $n = 20$), but for macroscopic charcoal the correlation is weaker ($r = 0.28$, not significant at $p < 0.05$ level) due to a relatively long period across the boundary of zones CC2 and CC3 when local fires were infrequent or absent from the bog surface. This suggests that the microscopic charcoal signal from this part of the core is regional, and that burning of *Calluna* was taking place across the reserve.

Regional vegetation history

There are broad similarities between the profiles for the two sites which provide further insight into regional vegetation change at Abernethy Forest, particularly when considered with previously published profiles for the area (Fig 5.3). Both pollen profiles particularly resemble O'Sullivan's (1974a) sequence from Loch Garten, although most of the basal zone he identified as being early Holocene is missing from the NA and CC sequences (Fig. 5.2). Zone assemblages from NA1 and CC1 resemble the *Betula-Corylus/Myrica* zones from other regional profiles in the area, in particular from Abernethy Forest (Birks and Mathewes, 1978), and Loch Garten and Loch a'Chnuic (O'Sullivan, 1974a). From the correlation, the estimated age of the upper zone boundary for NA1 and CC1 is *c.* 8400 cal. BP (7500 BP; Fig. 5.2). Birks (1970) suggested that high presence of *Corylus/Myrica* pollen in this regional zone means it occurred as a canopy, rather than an understorey, species. Examples of such communities in the Scottish Highlands are rare today, but modern pollen samples from small remnants of semi-natural woodland with a *Betula/Corylus* canopy on Skye produce similar assemblages so are potential modern analogues (Birks, 1973, 1980).

Relative to the *Betula* pollen curve, which peaks just above the base of the core before rapidly declining, the increase in percentage *Pinus* pollen in zone CC2 (estimated at 7500

cal. BP ; 6500 BP) seems to have occurred more rapidly than at sites NA and Loch Garten (*c.*8400 cal. BP). This rapid rise is also seen in O'Sullivan's (1974a) profiles from Loch a'Chnuic, and suggests *Pinus* colonised the well-drained slopes of the Carn a'Chnuic area more readily than the wetter, lower lying areas around North Abernethy and Loch Garten. Independent dates would be required to establish this and to ascertain whether accumulation began at around the same time in the NA and CC basins. The general trends for both profiles are similar, and once established, *Pinus* appears to have remained the dominant taxon throughout.

Changes in stratigraphy and pollen proportions seen in zone NA1c at site NA are similar to those of zone LC3 of O'Sullivan's (1974a) Loch a'Chnuic profile, where a series of banded muds is also recorded. This suggests that standing water may have become more widespread across the region *c.* 8900 to 8400 cal. BP (8000-7500 BP), possibly due to a rise in water table resulting from increased wetness related to climate change. It is likely that the pollen deposited during this period has a different taphonomy from previous or subsequent zones. As well as the atmospheric component, there may have been a much greater water transported component, such that the pollen records from both sites would have reflected the surrounding plants in a different way from previously. Representation of plants that have poor atmospheric pollen dispersal *e.g.*, those that are insect pollinated or cleistogamous (self-pollinating in the bud) may have increased.

This was not discussed by O'Sullivan (1974a), but may in part account for the increase in *Empetrum* proportions at NA. *Empetrum* pollen is not well-dispersed in the atmosphere and the plant has a preference for well-drained areas such as hummocks and gully sides (Tallis, 1997). Its pollen may therefore have been water-transported with flood-borne sediments into the NA basin from higher ground. The possibility of mixing and reworking of older pollen by surface water processes therefore cannot be excluded. An increase in the proportion of *Corylus*-type pollen is also seen within the detrital muds in O'Sullivan's Loch a'Chnuic (1974a) profile, suggesting that the presence of *Corylus* had increased in the wider surrounding vegetation or, more probably, that this pollen is *Myrica gale* from a fen community similar to that suggested for the NA sequence.

The start of zones CC2 and NA2 can be correlated with the start of zones LC4 at Loch a'Chnuic, LGD at Loch Garten (O'Sullivan, 1974a) and AF-4 and AFP6 from Abernethy Forest (Birks, 1970; Birks and Mathewes, 1978). This would date the base of this zone to *c.*

8400 cal. BP (7500 BP; Fig. 5.2). At both NA and CC the process of basin infilling may have made local conditions more favourable for *Pinus* by this time, with stomata presence indicating local growth in NA2.

If the inferred age of *c.* 7800 cal. BP (7000 BP) for the first arrival of *Alnus* at North Abernethy is approximately correct, it occurs slightly earlier than is observed at Loch Pityoulish, Loch a'Chnuic and Loch Garten (O'Sullivan, 1974a; 1976) but this may be an artefact arising from the lower counts used for this study. Alternatively, it may be a result of the close proximity of favourable habitat in the Spey and Nethy valleys and their tributaries. Evidence from NA and CC supports the idea that its expansion to a more or less stable proportion did not take place until well after the first *Pinus* maximum, as observed in other parts of the Highlands. The *Alnus* rise appears to correspond with or closely follow with a wet episode between 7200 and 6600 cal. BP (6250 -5800 BP) identified by Dubois and Ferguson (1985), which would have increased the availability of suitable habitat. By comparison with other regional profiles, the onset of local presence can be approximated at 6600 to 6400 cal. BP (5800-5600 BP) for both sites. By this time, *Pinus* pollen percentages have reached their maximum at all sites (Fig. 5.2).

Pine decline

There is no firm evidence for a 'pine decline' in either the NA or CC profile, but a higher sampling resolution would be needed to better assess this for CC. Regarding the possibility of a 'tephra effect', if all cores are compared for *c.*4260 cal. BP, it can be seen that there are similar marked but apparently temporary changes at NA (zone NA3/NA4) and Loch a'Chnuic (LC6). At both sites, there is a sharp decline in percentage *Betula*, *Alnus* and *Corylus*-type pollen followed by a decline in percentage *Pinus* pollen, which suggests that there may have been some tephra effect, but that it did not affect all sites. A temporary decrease in *Pinus* pollen is also seen in the lower section of zone LGA at Loch Garten, which O'Sullivan (1974a) interprets as early clearances around Loch Garten. Taking into consideration the error for the radiocarbon date (4236-3689 cal. BP; 3635±205 BP) it is not inconceivable that clearances were related to the Hekla-4 tephra fall, and were more widespread than was first suggested.

The changes observed may have resulted from forest die-back caused by the tephra fall-out itself. The effects of tephra falls on vegetation are still under debate, but dendrochronological evidence for inhibited tree growth during the period after volcanic eruptions suggests that

volcanic ash can persist in the atmosphere for as long as ten years, obscuring light and triggering wetter conditions that may trigger tree death in marginal habitats (Baillie and Munro, 1988). Following clearance of atmospheric dust, it may be that *Betula* was able to invade gaps created by tree death more rapidly than *Pinus*. The abundance of dead wood may also have contributed to the increase in charcoal abundance through increased availability of fuel.

From hydrogen isotopes in pine stumps, Dubois and Ferguson (1985) identified another period of higher rainfall between 4700 and 4400 cal. BP (4250-3850 BP), which may have been related to greater activity on the Polar Front (Whittington and Edwards, 1997) or possibly the tephra fall itself (Blackford *et al.*, 1992). No changes in stratigraphy are observed at this point in the NA profile, but there is a sustained peak in *Sphagnum* (as a percentage of TLP plus spores; Appendix 2a) that may indicate a local increase in wetness.

Whatever the causes of these changes, the recovery of *Pinus* to former levels does not suggest that this was a 'decline'. Rather, it seems to represent a disturbance caused by an external factor or more likely a combination of related factors such as the Hekla-4 tephra fall, short-lived climate change and human activity.

Regional fire history

The cyclical charcoal patterns and pollen diagram correlation (Figs. 5.4 and 5.5) suggest that fire events increased in intensity and frequency around or shortly after the *Pinus* maximum (7500-6800 cal. BP; 6500-6000 BP). These patterns are consistent with human use of fire, although with pine forest the dominant ecosystem, natural causes cannot be entirely excluded. The period between cycles where charcoal is low or virtually absent is estimated at *c.* 5700 to 4600 cal. BP (5000-4000 BP), which may indicate wetter climatic conditions in the region.

From *c.* 3800 cal. BP (3500 BP), there is a gradual increase in the C:P index and macroscopic charcoal abundance, particularly at NA, suggesting that human fire activity was intensifying from this time as heathland developed. Local fire appears to have been important at NA over the past few hundred years, but is not indicated at CC during this period. NA is situated closer to the focus of commercial forestry activities and human settlement than CC, which may have increased the likelihood of accidental fires.

Heathland formation

The increase in percentage *Calluna* pollen seen across all sites from *c.* 4300 cal. BP (3800 BP) supports O'Sullivan's (1974a) interpretation that this represents the start of heathland formation. Birks (1970) suggested that this steady rise in *Calluna* pollen and shade intolerant herbs such as *Plantago lanceolata* reflected a reduction in forest cover and a degree of farming activity. These changes appear to have been widespread throughout the region. Zone LC5 at site CC records *Pinus* pollen at its lowest value since its initial establishment, and from the microscopic charcoal record this seems to have been associated with high frequency and/or intensity of burning at a regional scale, consistent with human activity.

The NAP zones (NA4 and CC4/CC5) show similar trends to those seen in other profiles from the region, although the increase in *Calluna* pollen is more pronounced in O'Sullivan's (1974a) core from nearby Loch a'Chnuic. Here, there are three further phases in the expansion of *Calluna* pollen which O'Sullivan (1974a, 1977) compared with historical records. He suggested they represented changes in nineteenth century farming practices which resulted in a change from forest to heathland and back to forest in the space of two hundred years. The dominance of *Calluna* in the forest field layer today suggests that such changes in land use have affected the composition as well as the extent of the forest communities (O'Sullivan, 1977).

Recent increases in *Pinus* pollen percentages are probably associated with increased planting of *Pinus* since the mid eighteenth century and are seen in NA5, CC6 and LC10 at Loch a'Chnuic, suggesting that the base of zones CC6 and NA5 date from at least the last three hundred years.

Discussion

Strengths and limitations of study

Several points emerge that need to be considered when interpreting these results. First of all, although the tephra was a useful isochrone and correlation with existing profiles was possible, obtaining radiocarbon dates for key events such as the onset of changes in fire regimes and the arrival of *Pinus* and *Alnus* is a priority. In order to establish the first arrival of *Pinus* and *Alnus* with greater confidence, a higher count and smaller sampling intervals are needed and it may be that the arrival of *Alnus* predates the start of sediment accumulation.

A closer sampling interval would have been desirable to give a better indication of the variability of the pollen signal over time, but for the purposes of identifying major vegetation units and gaining an idea of fire history for a region where several dated profiles already exist, these analyses have provided useful new information. The sharp changes seen in NA1c and NA3b may be functions of the closer sampling interval at these parts of the profile rather than being true anomalies, but both sets of changes were also recorded by other profiles from the region so this is probably not the case.

Further work

At both sites it seems that fire has been an important part of the ecosystem since *Pinus* first rose to dominance, but not consistently through time. Periods of low local and regional charcoal abundance seem to correlate with wet shifts, suggesting that climate was an important modulator of fire regime. A recent multi-proxy palaeoclimate study from Tore Hill Moss, Abernethy Forest, shows that at least seven wet shifts have occurred since *c.*2510 cal. BP (Blundell and Barber, 2005). Further independent climate proxies with matching pollen and charcoal records would be useful to further investigate the relationship between climate and fire regime.

Further studies of the relationship between fire and charcoal production, *e.g.* to investigate the effects of convection and varying fire intensities (*sensu* Clark, 1988a), may enable more robust interpretations of charcoal records, particularly in relation to the effects of particle size on dispersal and deposition. These studies of both macroscopic and microscopic charcoal show that the abundance of microscopic charcoal in some cases increases where *in-situ* fires are indicated, whereas in other cases it does not. The criterion for local fire of >50 particles per cm^3 in the 150-250 μm size class was derived from observations by Whitlock and Larsen (2001) but a wider range of studies is needed to allow its general appropriateness as an indicator to be assessed.

More research is needed into the taphonomy of tephra in peat, as clearly it has important implications for this type of work (Hall and Pilcher, 2002). In a pioneering experimental study, Payne *et al.* (2005) applied tephra of different shard sizes to peat surface plots, and observed that smaller shards were more able to migrate downward through smaller pores in the peat matrix, whilst larger shards remained nearer to the surface. Over a two year period they observed secondary peaks and downward 'tails' in several samples which they suggest

may be related to the vegetation and microstructure of the peat, particularly its porosity and the existence of vertical internal channels. Further work is needed to establish how pollen and charcoal may be affected by such factors, and what the role of particle size and morphology, particle density and peat microstructure may be. For sequences without tephra, there may be no way of telling what degree of disturbance may have taken place.

Summary

From these results, it appears that there was a change in conditions around 9500 cal. BP (8500 BP) that led to tree death and the onset of sediment accumulation in both basins, probably in response to a wet shift. It is apparent that the pine forest was well-established by *c.* 6800 cal. BP (6000 BP), with a series of regional oscillations having occurred between then and the present day. There is little evidence for a 'pine decline' at either site but there may have been a relatively short-lived regional 'tephra effect' *c.* 4260 cal. BP from which the vegetation was able to recover. Fire seems to have played an important but inconsistent role in landscape development, with long periods of little or no activity during wetter phases. Human firing of the landscape possibly started near Loch a'Chnuic in the Mesolithic as early as 6800 cal. BP (6000 BP), at which point heathland formation appears to have been reversible. Fire was closely associated with apparently more permanent heathland formation from *c.* 4300 cal. BP (3800 BP). These changes require further study to detect variations in site development at a smaller scale and this is the subject of the following chapter.

Chapter 6. Abernethy Forest: a history of the past 5000 years from multiple profiles

Introduction

Existing palaeoecological records for the Abernethy Forest region mainly record regional vegetation change, (*e.g.* Birks, 1970; O'Sullivan, 1974, 1976; Birks and Mathewes, 1978). The aim of this chapter is therefore to explore long-term vegetation dynamics using palaeoecological records that reflect the surrounding vegetation at a smaller spatial scale that is more relevant for ecology (*sensu* Sugita, 1994). Pollen, *Pinus* stomata, peat stratigraphy and charcoal records will be used to reconstruct individual basin histories, then the results compared between sites to explore local temporal and spatial variations in vegetation development.

The focus is on changes over the past 5000 years to explore changes since human activity in Scotland first intensified (Edwards and Whittington, 1997). This presents challenges for vegetation reconstruction as human activity has spatially and temporally unpredictable effects on the landscape and once a 'cultural landscape' emerges, the methods used to study it need to take account of increased patchiness (Birks, 1986, 1988; Tipping, 1994). Detecting such variation in the landscape requires multiple sites that reflect the surrounding vegetation at a smaller scale. If the vegetation type and forest composition can be established for a network of sites around the reserve, this will give a fuller picture of spatial variations in past vegetation cover. It would also give insight into the effects of disturbance and an indication of the timescale over which current vegetation patterns have developed.

This chapter presents five new bog sequences from the Abernethy Forest Reserve which are correlated using Holocene tephra deposits. Local pollen assemblage zones are identified, for which age estimates for zone boundaries are obtained by comparison with existing published work pending the outcome of a radiocarbon dating application. Individual site development histories are then presented and compared between sites. Changes in forest composition and openness, the long-term dynamics of heathland development and the long-term fire regime are discussed, with particular emphasis on understanding more of the long-term fire history and impact of human activity throughout the reserve.

Vegetation history and human activity in the Central Highlands

The early post-glacial development of vegetation in Scotland is reviewed in chapter 1. A brief summary is given for the Central Highlands region from *c.* 6800 cal. BP (6000 BP) with particular reference to human activity.

Until *c.*6000 cal. BP, the forests of the Central Highlands appear to have developed with very little human influence. In general there is little evidence for the activities of Mesolithic people and their impact on the forest is presumed to have been small (Tipping, 2003). Mesolithic sites are difficult to detect as they consist mainly of tool scatters but large quantities of flints have occasionally been found, *e.g.* along river valleys in Deeside, Banffshire and Kincardineshire (Finlayson and Edwards, 1997).

From 6800 to 6400 cal. BP (6000-5500 BP), a wetter climate and rising water tables are associated with a rise in *Alnus*, which would have colonised wet valley soils (Tallantire, 1992; Bennett and Birks, 1990). From *c.*6400 cal. BP, it is likely that humans were settling around fresh water lochs and subsequently began to clear the surrounding forest for grazing, encroaching further inland along the Dee, Don and Spey valleys (Grant, 1994; MacKenzie, 2002). The pine forest was probably still at its maximum extent until *c.* 5700 cal. BP (5000 BP; Bennett, 1984; Birks, 1988). By 4600 cal. BP (4000 BP), *Pinus* was restricted to northern and mountainous areas and its range was further reduced around this time by the spread of blanket bog (Bennett, 1984). This regional 'pine decline' is often attributed to anthropogenic impact (Bennett, 1995), although climate change may also have played a major role.

Archaeological evidence from *c.* 4600 cal. BP , *e.g.* the Clava cairns, enclosures and stone circles of the north east coastal regions of Scotland, is associated with a transition from hunter-gatherers to a more settled economy (Tipping, 2003). Neolithic and Early Bronze age impact on the forests of the Highlands was probably variable, but population pressure was probably lower in more inaccessible areas of the Cairngorms and there seems to have been little human impact on the forest in the Central Highlands during this early settlement period (Grant, 1994; Edwards and Whittington, 1997; MacKenzie, 2002). By the beginning of the Iron Age (*c.* 2900 cal. BP; 2800 BP), it seems that the decline in forest cover across Scotland that continued until the eighteenth century was already well advanced, but that thus far, forest composition was relatively unchanged. However, the pollen evidence from this period is difficult to interpret, as practices such as coppicing and pollarding would have inhibited

pollen production whilst not necessarily constituting clearance (Armit and Ralston, 2003). It is likely that the substantial forest clearance that began in the Bronze Age (4600 cal. BP-2900 cal. BP; 4000 BP-2800 BP) continued along more fertile, hospitable river valleys (MacKenzie, 2002). The practice of transhumance may have contributed to the transition from forest to heath in some upland areas (see Pears, 1967).

Whilst there is some evidence that forest regeneration took place in some previously farmed areas *e.g.* at Abernethy Forest (O'Sullivan, 1977), it seems that in general a more open landscape developed until at least the beginning of the early medieval period *c.*1500 years ago. From this period, Crone and Watson (2003) argue that forest cover may once again have increased due to reduced agricultural activity and settlement retraction. However, Smout (1997) argues that farming practices and climatic deterioration beginning around 4300 cal. BP (3800 BP) resulted in loss of most of the forest by 1000 cal. BP (1000 BP). It is therefore possible that extensive deforestation had already occurred by the time commercial exploitation escalated in the mid-eighteenth century. Historical evidence for this period suggests that the remaining forest was largely confined to highland areas, with patchy persistence in the lowlands, including along river valleys (Stewart, 2003). As a result of the lack of timber resources and a desire to manage the landscape for game and amenity purposes, the practice of tree planting emerged across most of Scotland in the eighteenth and nineteenth centuries (House and Dingwall, 2003). The quest for appropriate management techniques remains an important issue, but the focus has now shifted towards conservation of the remaining small fragments of semi-natural pine forest, as it is estimated that only 1% of the original forested area remains (JNCC, 2006).

Vegetation dynamics and human activity at Abernethy Forest

Heathland development

O'Sullivan (1973a) studied seven mor humus profiles dating from *c.* 1500 cal. BP (1500 BP) to investigate recent heathland dynamics at Abernethy Forest. Radiocarbon age estimates for the beginnings of heathland formation ranged from AD 450 to AD 900, so O'Sullivan (1973a) suggests that it did not occur during a single period. McVean and Ratcliffe (1962) and McVean (1963) suggest that initial clearances occurred around AD 400 in association with an influx of Iron Age Picts, and were followed by a gradual increase in the amount of heathland due to burning and light grazing lasting until around AD 1000.

This was seen as marking the onset of a dynamic relationship between pine forest and moorland that may have continued until the present day. O'Sullivan (1973a) found that some sites that currently support pine forest had in the past been areas of open moorland. Near Loch an Spioraid (Fig. 6.1), changes in percentage pollen of *Pinus*, *Betula* and *Calluna* were interpreted as successive colonisation of an initially open heathland by *Pinus* forest. Using tree coring, a date of AD 1870 was estimated for the existing *Pinus* stand. In some locations it therefore appears that open conditions prevailed until *c.* AD 1840, when planting is known to have occurred (O'Sullivan, 1973a).

This evidence suggests that pine forest can re-establish on formerly open areas and that heathland dynamics (and therefore levels of human activity) were variable across the reserve, but as mor humus develops beneath the canopy the sites investigated reflect highly local changes so may not be representative of wider scale heathland dynamics. O'Sullivan (1973a) also pointed out that mor humus is not ideal for pollen studies as decomposition, mixing and removal of material may occur. He was therefore unable to be confident that gradual changes in the pollen profile reflected actual vegetation change. At the base of some of the profiles, pollen evidence indicated that past forest vegetation may have been more diverse, with greater proportions of *Betula*, *Corylus* and *Alnus*. Analysis of sequences containing records from a longer time span is required to understand the development of heathland more fully.

Fire history

Other than inferences about fire regime made from previous studies of heathland development, little is known of fire frequency and rotation at Abernethy prior to the mid-eighteenth century. From this period there is anecdotal and historical evidence for large fires in 1746 and 1770 (O'Sullivan 1973b; Proctor, 1998). There is some evidence from charcoal profiles that fire has decreased in frequency in the recent past (Cavalho, 1999; see chapter 2), which may correspond to the past few hundred years when fire was suppressed to protect valuable timber yields.

Fire proxies are needed for Abernethy Forest to learn more about the fire regime and how it may have affected vegetation at both regional and local scales. Such information will assist future management decision-making concerning the control and manipulation of fire (see also chapters 2 and 8).

Archaeology

As both population and land use intensity are low in Abernethy Forest, archaeological features are seriously under-recorded. Wordsworth (2003) points out that damage by forestry practices and the problems of locating sites within an often dense field layer also make recording difficult. He noted that although only six sites are recorded in the Highland Council's Sites and Monuments Record for the reserve, documentary records indicate that there are at least 173 additional sites within the reserve boundary. In 1995, a field survey targeted on an Ordnance Survey kilometre square at Rynettin (National Grid Reference NJ 0114) revealed 20 new sites, including two chambered cairns and a prehistoric enclosure, the latter being the only evidence for prehistoric settlement recorded in the area to date. In future, if more information on the types and distribution of archaeological sites in the reserve becomes available, this could be studied alongside palaeoecological records to increase understanding of human impact on the landscape at Abernethy Forest.

Aims

A palaeoecological study was undertaken to address some of the gaps in current knowledge of smaller scale vegetation changes within Abernethy Forest over the past 5000 years. The aims were to further understand i) timing and location of changes in forest composition and openness; ii) the onset and long-term dynamics of heathland development, including heathland-pine forest transitions; iii) changes in the long-term fire regime at regional and local scales. This was carried out by collecting and interpreting stratigraphic, stomata, pollen and charcoal records from a network of five sites. Site histories are interpreted then the results are compared for all sites.

Study area

See chapter 1 for a full description of the Abernethy Forest reserve and the 15 km x 15 km study area within which the sites were located.

Site selection

As the period of interest for this study was the past 5000 years, basins with shallow sediments were considered, giving preference to sites with more than 1 m depth of peat. Well-defined sedimentary basins of small to medium size (60 m - 200 m diameter) were chosen as these were more likely than large basins to have recorded local pollen (see

Jacobson and Bradshaw, 1991; Sugita, 1994). The charcoal source area of such sites is also likely to be more limited (Clark, 1988a), making such sites ideal candidates for studies of

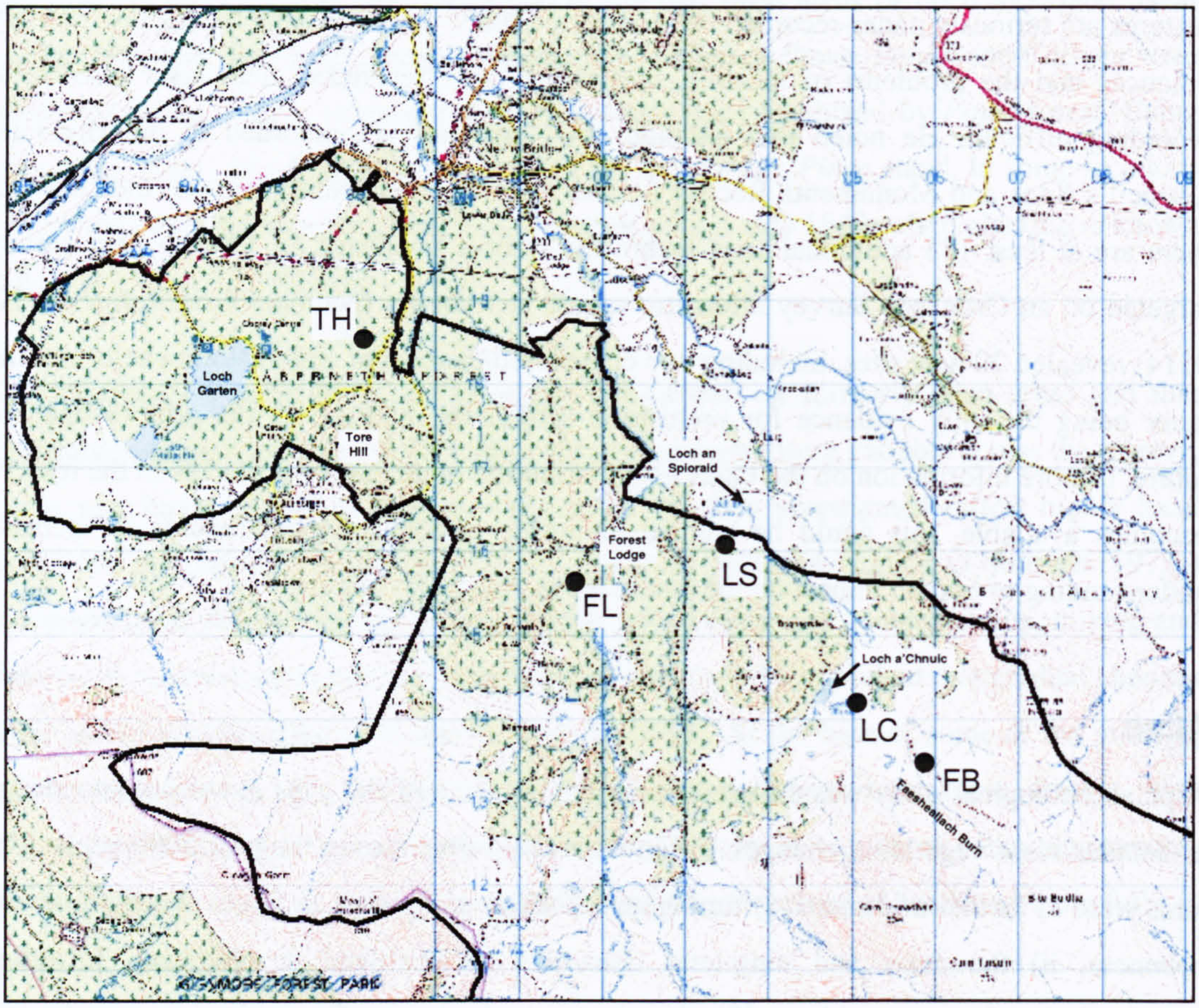


Fig. 6.1. Location of cores from Abernethy Forest: TH = Tore Hill; FL = Forest Lodge; LS = Loch an Spioraid; LC = Loch a'Chnuic; FB = Faesheallach Burn. The black line shows the reserve boundary.

fire history. Where possible sites were spaced around 1-2 km apart and located on both forested and open areas throughout the reserve.

There have so far been relatively few palaeoecological studies of Scottish blanket bog sequences (*e.g.* Birks, 1975; Bennett *et al.*, 1990, 1992; Charman *et al.* 2001) and none so far in Abernethy nature reserve. Whilst blanket bog pollen sequences may be affected by complex hydrological processes and sediment instability (*e.g.* Warburton *et al.*, 2002; Holden and Burt, 2004), with careful site selection it was considered feasible to use them to explore vegetation history further in what is now a more open area of the reserve.

From within the present day forested area, two basins were selected near Tore Hill and Forest Lodge (sites TH and FL; Fig 6.1; Table 6.1). Site TH is an excellent example of an

Table 6.1. Location and description of core sites around Abernethy Forest.

Site name	Grid Ref.	Description	Site code	Basin type/size	Sediment depth (cm)	Description of base
Tore Hill	NH 992 185	West of Duack Burn	TH	Ombrotrophic mire 150 m x 100 m	600 cm (auger) 435 cm to wood (Russian sampler)	Widespread firm timber layer
Forest Lodge	NJ 016 162	0.5 km north west of Forest Lodge	FL	Largely intact forest mire 100 x 200 m; opening 60 m x 60 m	200 cm to wood	Woody fragments, widespread firm timber layer
South west of Loch an Spioraid	NJ 032 161	North of area continuously forested since 1750	LS	Linear mire running west to east *c.* 50 m from forest edge; 100 m x 200 m	Uniform *c.* 150 cm	Bedrock; woody fragments
East of Loch a'Chnuic	NH 051 142	200 m east of Loch a'Chnuic	LC	Blanket bog, shallow depression 70 m x 70 m	Uniform, *c.* 130 cm	Bedrock, sand recovered
East of Faesheallach Burn	NJ 058 134	1.5 km south east of Loch a'Chnuic	FB	Blanket bog, shallow depression 70 m x 70 m near south west edge of 500 m x 500 m plateau	Uniform 200 cm to wood	Woody fragments, widespread timber layer.

ombrotrophic raised bog within the more densely forested northern part of the reserve. It appears to have been surrounded by forest at least since historical records began in AD 1750, except when timber extraction in first half of the nineteenth century left very little forest west of the River Nethy (O'Sullivan, 1973b). The current opening around the core site is approximately 150 m x 200 m diameter, and the apparently undisturbed parts of the bog surface have scattered, stunted *Pinus*. Site FL is a small forest bog near the RSPB reserve office in the more densely forested part of the reserve, *c.* 0.5 km west of the River Nethy which, like TH, appears to have been surrounded by forest since historical records began. The surrounding forest is dominated by *Pinus*, and *Vaccinium* is abundant on the bog surface. The current opening is *c.*60 m x 60 m, although the sedimentary basin itself extends to *c.*150 m x 100 m.

A third site (LS) is located to the south of Loch an Spioraid (Fig. 6.1), 100 m due west of the stand of *Pinus* from which O'Sullivan (1973a) obtained a mor humus profile. In order to

investigate the longer term status of the apparently cyclic heathland-forest system he identified, this sequence was collected from an adjacent mire, around 50 m north of the edge of the current *Pinus* tree line (Table 6.1).

Two open blanket bog sites, East of Loch a'Chnuic and East of Faesheallach Burn (LC, FB; Table 6.1), were selected from shallow depressions as these were considered less likely than sloping areas to have undergone disturbance. Site LC was within a basin *c.* 70 m x 100 m, *c.* 0.5 km east of Loch a'Chnuic, where peat sediment overlays sand and rock. Site FB was within a *c.* 70 m x 70 m basin located *c.*1 km to the south east. Buried stumps were frequently encountered at *c.*200 cm depth during the initial auger survey.

Site selection was thus designed to complement the regional sequences obtained from the larger bogs (see chapter 5), whilst attempting to obtain sites with some overlap in pollen source areas (estimated at *c.* 1190 m radius; see chapter 4) to facilitate landscape reconstruction.

Methods

Full details of all methods are given in chapter 2. The microscopic charcoal to pollen concentration ratio (referred to hereafter as the C:P index) was used as an indicator of 'real' fires (Swain, 1973). Macroscopic charcoal counts above 50 particles per cm^3 were interpreted as local fire events (see Whitlock and Larsen, 2001). All cores were taken in March and November 2004 and tephra geochemistry was determined at the Tephrochronological Analytical Unit at the University of Edinburgh. Pollen zones were decided subjectively based on end-groups from unconstrained cluster analysis carried out in *psimpoll v.4.10* (Bennett, 2002). For an explanation of the humification index referred to in the zone descriptions, see chapter 2, Table 2.2.

Results

Tephra

Ten tephra layers were detected using light microscopy, of which seven were successfully extracted and at least ten shards per sample were analysed for geochemistry. Full details of shard composition are given in Appendix 1b. Of the remaining three samples, one yielded no shards after acid digestion (FL, 18 cm), and two others from LC contained such high

concentrations of mineral material that no shards could be sufficiently exposed to allow geochemical analysis. Identification involved comparing the percentages of magnesium and

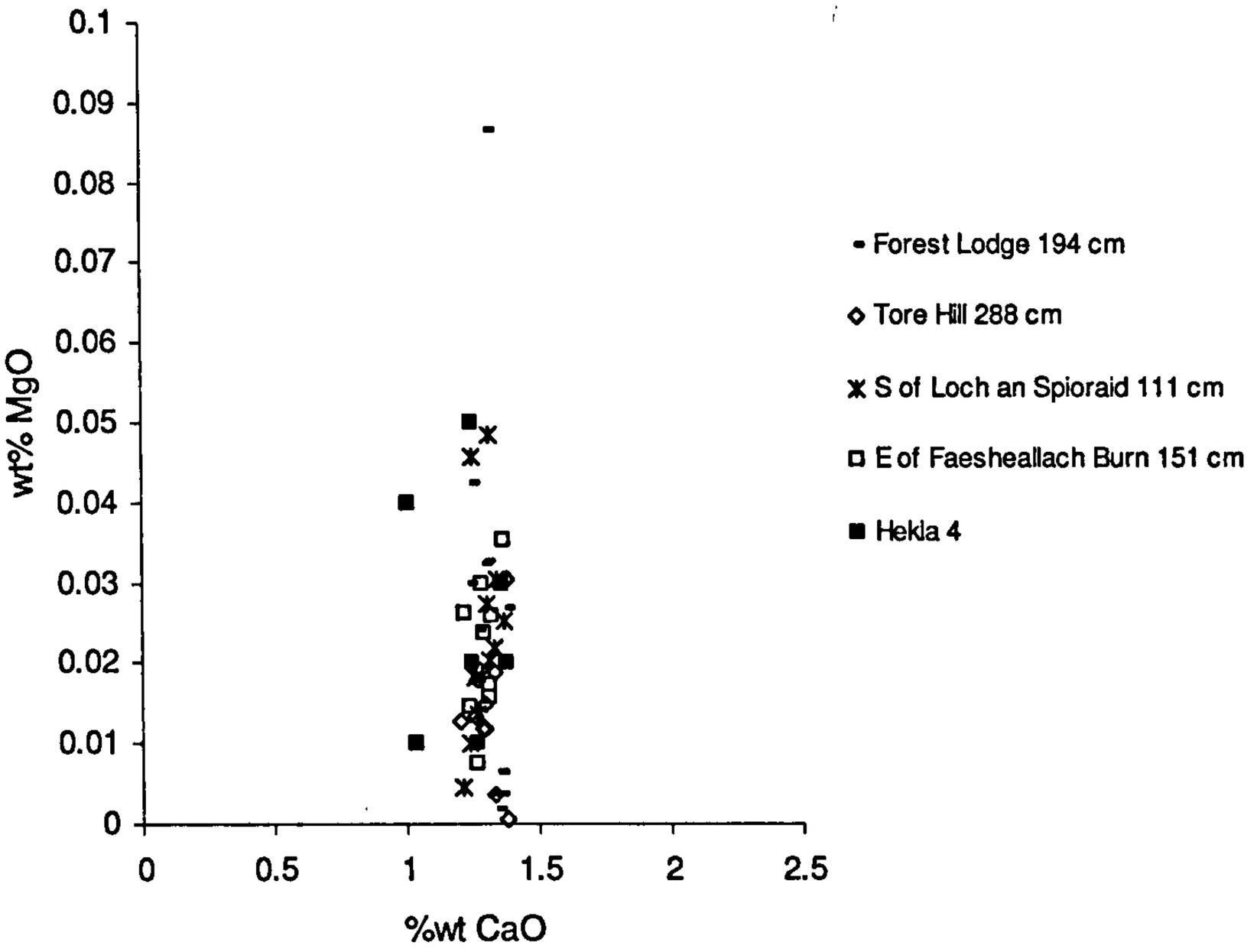


Fig. 6.2. Relationship between calcium and magnesium oxides for tephra layers in four profiles from Abernethy Forest, plotted with Dugmore *et al.'s* (1995) representative analyses of the Hekla-4 (*c.*4260 cal. BP) tephra.

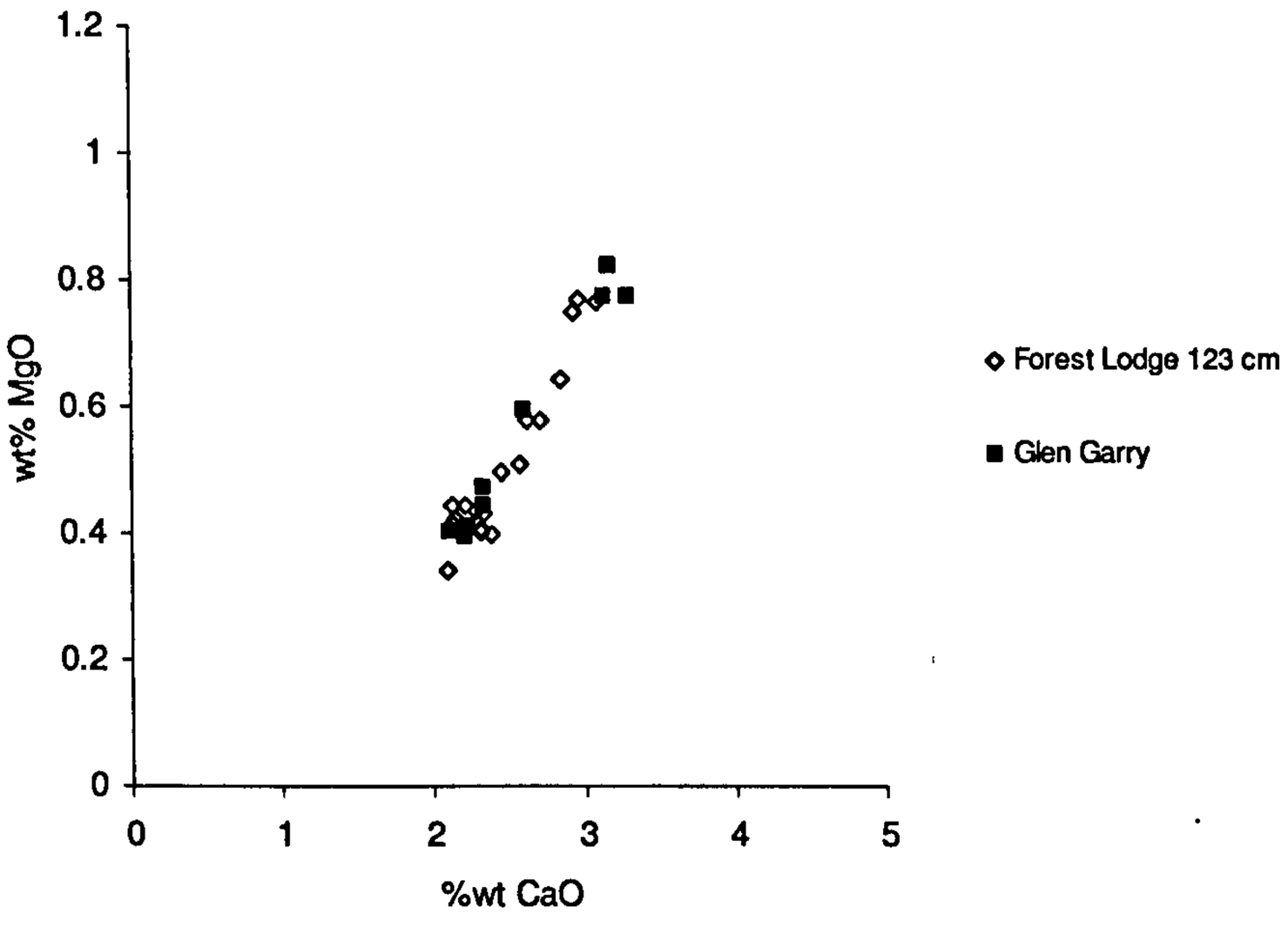


Fig. 6.3. Relationship between calcium and magnesium oxides for the Forest Lodge profile, plotted with Dugmore *et al.'s* (1995) representative analyses of the Glen Garry (*c.* 2150 cal. BP) tephra.

calcium oxides with that of representative shards of known reference tephras as published by Dugmore *et al.* (1995).

Tephra within the compositional range of Hekla-4 (*c.* 4260 cal. BP; 3830 BP) was identified in four of the five cores (Fig. 6.2). The presence of Hekla-4 in LC was inferred from shard morphology and stratigraphic position on comparison with tephra from nearby FB. Tephra comparable to the composition of the Glen Garry tephra (*c.* 2150 cal. BP; 2100 BP) was identified in FL (Fig. 6.3); its presence in LC was inferred from morphology and stratigraphic position.

Chronology

The Hekla-4 tephra is a clear marker for 4260 cal. BP for sites FL, LS and the blanket bog sequences LC and FB. In all cases, peak concentration occurred within several centimetres of peat. However, at site TH, below the peak at 280 cm there is a large amount of downward vertical spread to the base of the sequence at 435 cm, suggesting considerable disturbance (see Fig. 7.1, chapter 7). Whilst the upper limit of 280 cm can be tentatively used as a marker for 4260 cal. BP, the integrity of this sequence in general is questionable.

Pollen analysis

Pollen diagrams for the five sites are shown in Fig. 6.4 a- e, and a tentative correlation for on-site (stratigraphic) and off site (pollen percentage) changes between the sites is shown in Fig. 6.5. Visual inspection of the pollen diagrams shows quite different pollen profiles at each site. The record from sequence TH raises some interesting questions about the development of bog woodland so, despite the problem of tephra disturbance, it is included but is interpreted with caution. A general description of major pollen zones from the individual sequences is given below, followed by interpretation and discussion of all five cores in relation to the whole study area.

Zone descriptions

1. Tore Hill (TH)

This profile has five zones, TH1-TH5 (Fig. 6.4a).

TH1 (452-410 cm) *Pinus* I zone

In zone TH1, pollen concentration is at its highest for the whole sequence, and the proportion of *Pinus* pollen is at its maximum at the base the profile at *c.*95%, decreasing slightly to 90%

Tore Hill

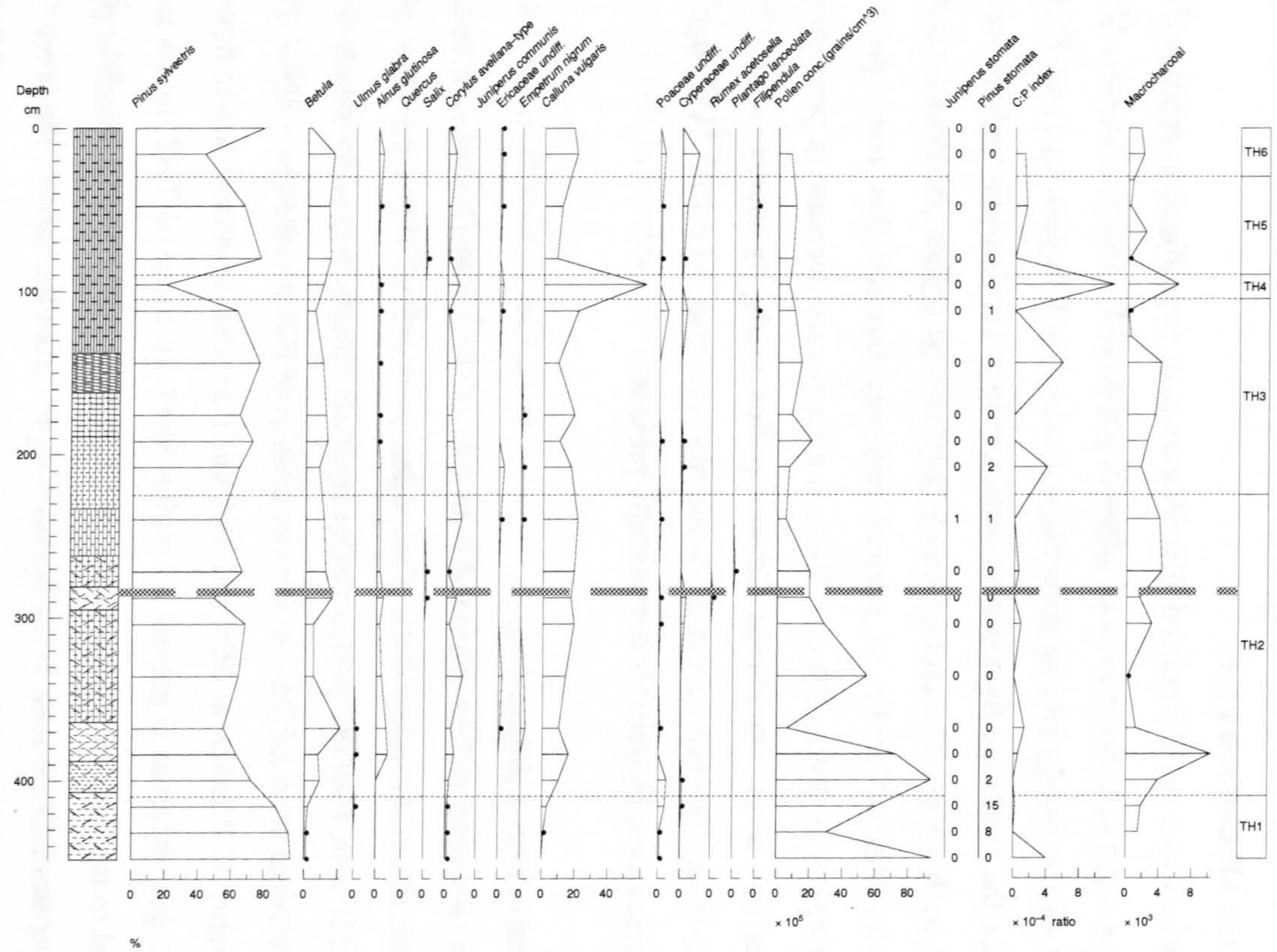


Fig. 6.4a. Summary pollen diagram from Tore Hill, Abernethy Forest. Percentages are based on Total Land Pollen. For key to stratigraphic symbols see Table 2.1, chapter 2. Macroscopic charcoal is measured as particles cm^{-3} in the 150-250 µm size class. Dots represent percentages less than or equal to 1%. The grey dashed line shows the position of the peak concentration of the Hekla-4 tephra deposit.

at the end of the zone. The matrix contains abundant partly humified wood fragments (humification index = 2) and frequent *Pinus* stomata are observed; no *Pinus* needle macrofossils are seen. *Calluna* pollen is not observed at the base of the profile, but a gradual increase in its percentage begins in the upper part of the zone, although levels remain low (up to 3%). Poaceae and Cyperaceae pollen are both present at low proportions (up to 4% and 1% respectively). Apart from a small peak in microscopic charcoal at the base of the core, both macroscopic and microscopic charcoal levels are low.

TH2 (410-225 cm) AP-*Calluna* zone

This zone comprises wet, well humified *Eriophorum* peat (humification index = 3) and is characterised by a consistent percentage of arboreal pollen (AP), mainly *Pinus* (*c.* 60%), and the continuation of the steady rise in percentage *Calluna* pollen seen in zone TH1. *Alnus* pollen appears for the first time then occurs consistently at levels of around 2%, reaching a maximum of 5% in this zone. The proportion of *Corylus*-type pollen also rises from that seen in TH1 to *c.* 5%. Hekla-4 tephra is present mid-way through this zone, providing an estimated age of 4260 cal. BP at 288 cm. There is a temporary decrease in percentage *Pinus* pollen to 50% at this level. Percentage *Calluna* pollen gradually increases to 20% in the upper part of this zone. The proportion of *Betula* also increases to *c.*10%. Although the C:P index is low, macroscopic charcoal is consistently present.

TH3 (225-105 cm) *Pinus-Calluna* I zone

The sediment in this zone is less saturated than that of TH2 and *Eriophorum* remains are more distinct (humification index = 2). The pollen record from this zone does not differ greatly from TH2, with *Calluna* pollen percentages remaining relatively steady at around 15%. The main change is an increase in the percentage of *Pinus* pollen to *c.* 65%. This zone also shows a higher C:P index at 208 and 144 cm than that observed lower down in the profile. Macroscopic charcoal is present at similar levels to those of TH2; levels are below the criterion used to indicate local fire events. A single *Pinus* needle macrofossil is present at 186 cm. No *Pinus* stomata are seen in the pollen samples from this part of the core.

TH4 (105-90cm) *Calluna* zone

This zone is represented by a single pollen sample, characterised by a much higher percentage of *Calluna* (65%). There is also a small increase in the proportion of *Corylus*-type pollen from 1% at the top of the previous zone to 7%. There is a sharp increase in the

C:P index and macroscopic charcoal in this level. Further counts would be needed to identify the vertical extent of this zone.

TH5 (90-30 cm) *Pinus II* zone

The sediment in this zone comprises partly humified *Eriophorum* peat (humification index = 2). No other type of plant material is seen. *Pinus* pollen percentages recover in this zone to levels similar to those in TH3, with *Calluna* pollen levels similarly falling to around 10%. Macroscopic charcoal and the C:P index are low in this zone.

TH6 (30-0 cm) *Pinus-Calluna* II zone

This zone comprises poorly humified *Sphagnum* peat (humification index = 1). The uppermost zone of the sequence shows a decline in the percentage of *Pinus* pollen to *c.* 40%, with an increase in both *Calluna* and Cyperaceae pollen values. The percentage of *Betula* pollen remains fairly consistent at *c.*15%. Charcoal levels show little change from those of TH5.

2. Forest Lodge (FL)

Six zones, FL1-FL6, are described for this sequence (Fig. 6.4b).

FL1 (200-198 cm) *Betula - Pinus* zone

This zone occurs in the basal 2 cm of the profile only, overlying a basal woody layer and containing abundant woody detritus in layers interspersed with darker sediment bands. Pollen concentrations are relatively high and there is very little charcoal. *Betula* pollen is dominant (*c.*70%), with some *Pinus* (*c.*15%) and *Alnus* (*c.*4%). There is very little *Calluna* pollen.

FL2 (198 -150 cm) *Betula-Pinus -Alnus* zone

In this zone the sediment is a partly humified *Eriophorum* peat (humification index = 2) with woody fragments (< 5 mm) decreasing upwards in size and abundance. No other plant macrofossils are seen. At the beginning of this zone there is an abrupt decrease in the percentage of *Betula* pollen to *c.*30%, and an increase in the percentage of *Pinus* pollen to over 40%. There is a rapid increase in the percentage of *Alnus* pollen, peaking at 55% TLP followed by a gradual decline. These changes can be dated to *c.*4260 cal. BP by the

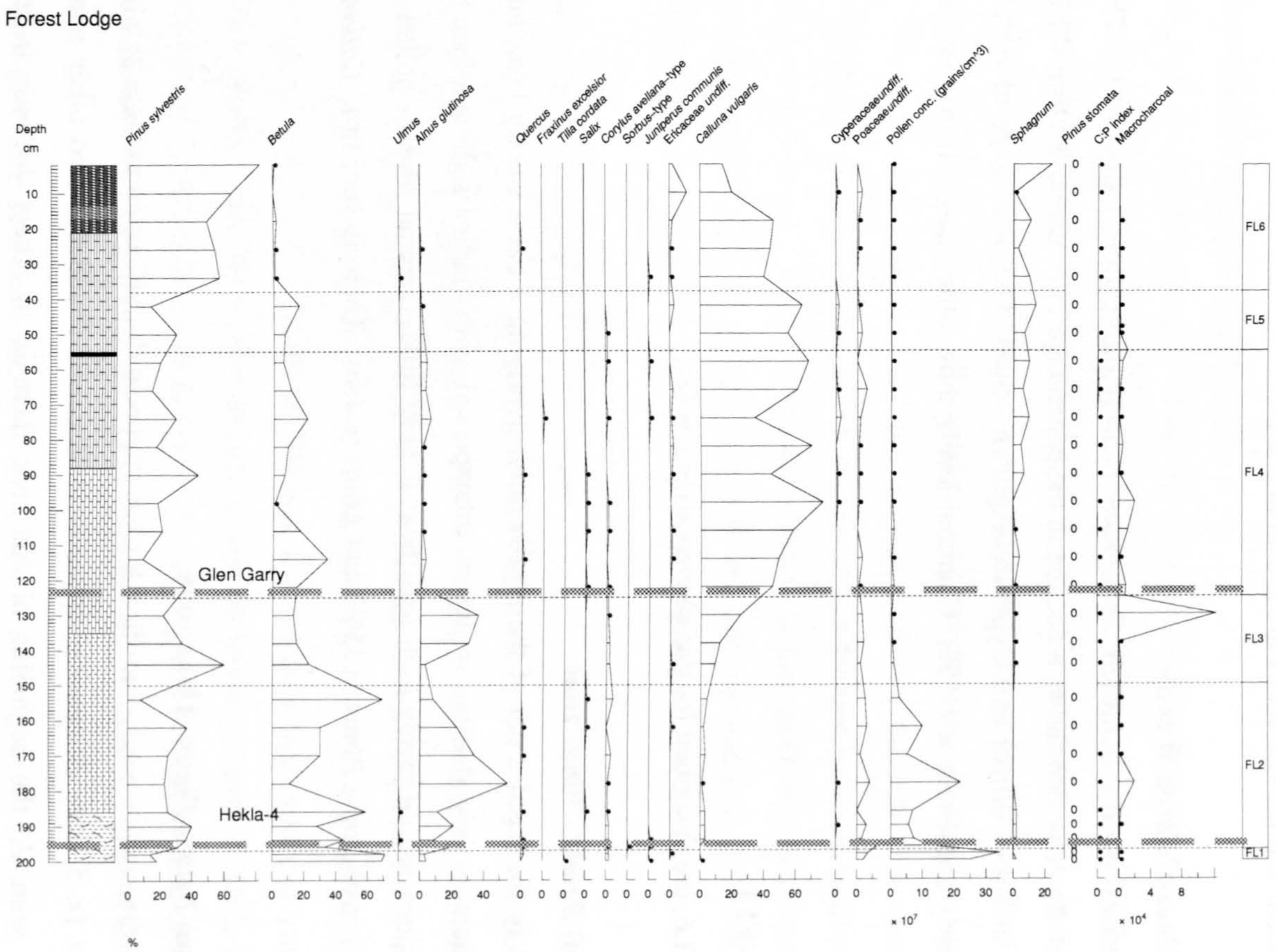


Fig. 6.4b. Summary pollen diagram from Forest Lodge, Abernethy Forest. Percentages are based on a Total Land Pollen sum (Total Land Pollen and Spores for *Sphagnum*). For key to stratigraphic symbols see chapter 2. Macroscopic charcoal is measured as particles cm^{-3} in the 150-250 µm size class. Dots represent percentages less than or equal to 1%. The grey dashed lines show the position of the peak concentrations of the Glen Garry and Hekla-4 tephra deposits.

occurrence of the Hekla-4 isochrone at the start of zone FL2. The overall proportion of arboreal pollen (*c.*90%) remains consistent throughout the zone. Charcoal remains at low levels.

FL3 (150-125 cm) *Pinus-Alnus-Calluna* zone

The sediment in this zone is *Eriophorum* peat (humification index = 2). This zone is defined by the start of a steady rise in the proportion of *Calluna* pollen from <10% to 25%. This is reflected in a decline in pollen concentration and a decrease in the percentage of *Betula* and *Pinus* pollen. *Alnus* pollen increases and peaking at 36%, almost returns to FL2 levels. At 130 cm, there is abundant macroscopic charcoal that fulfils the criteria for a local fire event, after which the percentage of *Calluna* continues to
rise. The end of this zone can be dated at 2150 cal. BP, as it coincides with the occurrence of the Glen Garry tephra isochrone.

FL4 (125-55 cm) *Pinus-Betula-Calluna* zone

The sediment in this zone is similar to that of FL3, becoming less humified (to humification index = 1) with decreasing depth. No remains from plants other than *Eriophorum* are visible. From this point in the profile, there is a sharp decrease in the proportion of *Alnus* pollen to around 1%, with no further recovery observed. Following the high charcoal peak in zone FL3 macroscopic charcoal occurs consistently but at low levels. The proportion of *Calluna* pollen continues to rise steadily, and there are greater frequencies of pollen taxa associated with open conditions, such as Cyperaceae, Poaceae and Rosaceae. The AP signal remains quite diverse, with *Quercus*, *Salix*, *Fraxinus* and *Corylus*-type appearing frequently at low percentages (<1%).

FL5 (55-38 cm) NAP zone

In this zone, the sediment remains *Eriophorum* peat, although less humified than in FL4 (humification index = 1). AP (mainly *Pinus* and *Betula*) is low at around 30%, with a decrease in the number of taxa observed. Non-arboreal pollen (NAP) taxa associated with open conditions remain frequent, *i.e.* Cyperaceae and Poaceae. The proportion of *Calluna* pollen remains steady at around 55-60%. There is a visible charcoal layer in the profile at the start of this zone (56-57 cm).

Loch an Spioraid

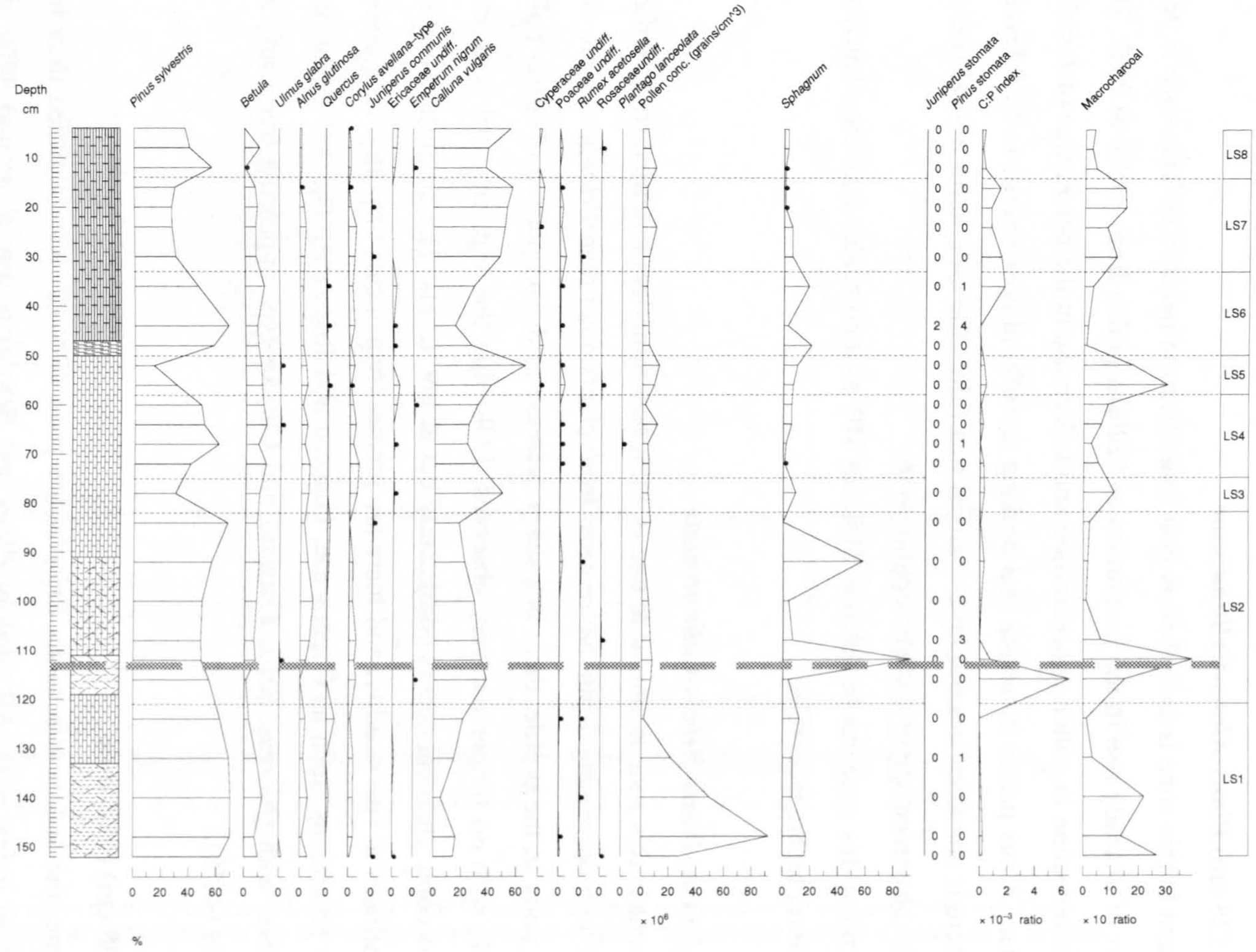


Fig. 6.4c. Summary pollen diagram from east of Loch an Spioraid, Abernethy Forest. Percentages are based on a Total Land Pollen sum (Total Land Pollen and Spores for *Sphagnum*). For key to stratigraphic symbols see chapter 2. Macroscopic charcoal is measured as particles cm^{-3} in the 150-250 µm size class. Dots represent percentages less than or equal to 1%. The grey dashed line shows the position of the peak concentration of the Hekla-4 tephra deposit.

FL6 (38-0 cm) *Pinus-Calluna* zone

Between 38 cm and 21 cm, the sediment comprises poorly humified *Eriophorum* peat (humification index = 1), changing to poorly humified *Sphagnum* peat at 21 cm (humification index = 1). Above 21 cm, the *Sphagnum* is only slightly humified (humification index = 0). *Pinus* pollen reaches its maximum proportions in this zone, rising from 56% to a present day maximum of 82%. The *Pinus-Calluna* ratio reaches its maximum, due to a notable decrease in the proportion of *Betula*; other AP taxa are largely absent. The proportion of Ericaceae *undiff.* pollen also rises to its highest level in recent times, but overall NAP shows a slight decline as the proportion of *Calluna* decreases to around 15-20%.

3. South west of Loch an Spioraid (LS)

This diagram was divided into eight zones, LS1-LS8 (Fig. 6.4c).

LS1 (152-121 cm) AP zone

Between 152 cm and 133 cm, the sediment is well humified (humification index = 3) with occasional recognisable Eriophorum remains and frequent wood fragments <1 cm in length. At 133 cm there is a distinct change to an open textured peat with abundant fibrous *Eriophorum* remains (humification index = 2) and occasional wood fragments. This zone is dominated by AP (>80%), with a fairly constant proportion of *Pinus* (60-70%) and consistent presence of *Betula*, *Alnus*, *Corylus*-type and *Quercus*. There is a relatively low proportion of *Calluna* pollen, increasing from *c.*15% to 20%. Other NAP occurs sporadically at low percentages, in the form of Poaceae, *Rumex* and Rosaceae. Pollen concentration is much greater in this zone than in subsequent zones. No *Pinus* needles are seen but *Pinus* stomata are present at 132 cm.

LS2 (121-82 cm) *Pinus-Calluna* I zone

This zone comprises well humified peat with some *Eriophorum* remains visible between 100 cm and 110 cm (humification index = 2). Above 91 cm a greater proportion of fibrous *Eriophorum* remains are visible. The zone is marked by an increase in *Calluna* pollen percentages, which peak at *c.* 40 % TLP. The presence of the Hekla-4 isochrone gives this increase an estimated date of just after 4260 cal. BP. There is a slight decline in the percentage of *Pinus* pollen to *c.* 50%. At 112 cm there is also a large peak in macroscopic charcoal. Microscopic charcoal peaks at 116 cm, corresponding with a slight decrease in the percentage of *Pinus* pollen at these depths. Subsequently, there is a small increase in

percentage *Pinus* pollen with corresponding decrease in percentage *Calluna* pollen which continues to 82 cm. NAP other than *Calluna* shows a similar pattern to that of zone LS1.

LS3 (82-75 cm) NAP I zone

This zone has similar sediment to the upper section of zone LS2, with in-situ fibrous *Eriophorum* remains (humification index = 2). This phase shows a sharp decline in the percentage of *Pinus* pollen and corresponding increase in *Calluna* pollen. There is little change in other AP taxa, with a peak in the macroscopic charcoal (112 particles per cm^3).

LS4 (75-58 cm) *Pinus-Calluna* II zone

Sediment is similar to that of LS3. There is an increase in percentage *Pinus* pollen and a decrease in percentage *Calluna* pollen and *Pinus* stomata observed at 68 cm. The proportions of *Betula*, *Corylus*-type and *Alnus* pollen remain consistent. There is a slight increase in the frequency of Poaceae pollen in this zone, but the proportion remains low (<1%). The pattern of microscopic charcoal changes slightly, with non-peaking concentrations being consistently higher than in previous zones.

LS5 (58- 50 cm) NAP II zone

Sediment is similar to that of LS3 and LS4. This zone shows a similar trend to zone LS3, with *Pinus* pollen levels dropping to 30% then 13%, with corresponding increases in the levels of *Calluna* pollen. Like the previous NAP zone, there is also an increase in macroscopic charcoal to levels associated with local fires, although at higher levels of up to *c.*300 particles per cm^3 at 56 cm.

LS6 (50- 33 cm) *Pinus-Calluna* III zone

There is an abrupt change in sediment at the start of this zone, where a distinct, 3 cm thick band of wet, poorly compacted peat is seen (humification index = 3), identified as *Sphagnum* peat under light microscopy. Above this, the sediment changes abruptly back to partly humified *Eriophorum* peat (humification index = 1). This zone comprises similar pollen assemblages to zones LS2 and LS4 with *Pinus* pollen percentages at 40-50% and *Calluna* percentages at *c.* 30%. *Pinus* stomata are present. Levels of macroscopic charcoal are reduced during this phase.

LS7 (33-14 cm) NAP III zone

This zone comprises *Eriophorum* peat (humification index = 1) characterised by a dominance of NAP, mainly *Calluna* pollen at over 50%, with percentage *Pinus* pollen below 30%. Levels of Poaceae and Cyperaceae pollen are slightly increased, but remain small (1-2%).

LS8 (14-0 cm) *Pinus-Calluna* IV zone

Sediment is similar to that of LS7. The start of this zone is marked by recovery in the percentage of *Pinus* pollen, initially to >50%, decreasing to *c.* 35% near the present bog surface. There is a decline in the concentration of macroscopic charcoal with the levels seen not meeting the selected criteria for local fire. Similarly, there is a decrease in the C:P index.

4. East of Loch a'Chnuic (LC)

This diagram was divided into six zones, LC1-LC6 (Fig 5.4d).

LC1 (128-106 cm) *Pinus-Betula* zone

Sediment in this zone is *Eriophorum* peat (humification index = 2), dry in texture with some fibrous remains and frequent woody fragments. This zone is characterised by consistently high percentages of AP at *c.* 95%. Two woody layers occur at 122-125 cm and 112-114 cm. *Pinus* and *Betula* are the main taxa, with *Pinus* pollen slightly dominant at *c.*40-50% and *Betula* pollen at *c.* 30-40%. The proportion of *Alnus* pollen shows a gradual decline from 20% to 4% at the top of the zone, whilst *Corylus*-type pollen percentages fluctuate between 1% and 5%. There were a few grains of *Ulmus*, *Salix*, *Quercus* and *Tilia* throughout the zone. Poaceae and *Calluna* pollen occur, but at low levels (1-3%). *Rumex* and Rosaceae pollen grains were occasionally seen. There is little charcoal.

LC2 (106 - 62 cm) *Pinus-Betula-Calluna* I zone

Sediment is similar to that of LC1. This zone is distinguished by the consistent appearance at higher percentages of both *Calluna* pollen (*c.* 5 -20%) and *Corylus*-type pollen (*c.* 5-15%). *Pinus* pollen becomes more dominant over *Betula* pollen. For a single sample at the base of this zone, there is a peak in the proportion of *Pinus* pollen (*c.* 75%). Similar peaks of *c.* 70% occur at 88 cm, 72 cm and 68 cm, whereas throughout the rest of the zone the percentage of *Pinus* pollen is around 45%. There is also a woody layer from 73-74 cm. *Ulmus* continues to occur as single grains, and *Rumex acetosella* and Rosaceae *undiff.* pollen grains occur at

similar levels to zone LC1. The Hekla-4 tephra isochrone at 96-98 cm gives this section of the core an estimated date of 4260 cal. BP, which coincides with a small peak in *Calluna* pollen and decline in *Pinus* pollen. Levels of charcoal remain low.

LC3 (62-46 cm) *Calluna* I zone

The peat in this zone is less humified than that of LC1 and LC2, with well preserved *Eriophorum* remains (humification index = 1). The zone is marked by a peak in the percentage of *Calluna* pollen from *c.* 30% at the top of the previous zone to *c.* 70%, after which it begins a decline to *c.* 10%. The number of NAP taxa is small, with just a few single grains of Poaceae, Cyperaceae and *Cirsium*-type. Ericaceae *undiff.* pollen is consistently present at low levels.

LC4 (46-38 cm) *Pinus-Betula-Calluna* II zone

Sediment is similar to that of LC3. The pollen assemblage zone bears some similarities to LC1, although *Betula* pollen counts are lower and decline from *c.* 15% to 10%. The dominant pollen taxa are *Pinus* (*c.* 40 - 45%) and *Calluna* (*c.* 40%).

LC5 (38-18 cm) NAP zone

There is no change in sediment in this pollen zone, which is characterised by a sustained increase in NAP to 65% with a corresponding decrease in *Pinus*. NAP is mainly *Calluna* but Cyperaceae and Poaceae pollen occur more frequently, with Cyperaceae reaching levels of 15% at 28 cm.

LC6 (18-0 cm) *Calluna* II zone

Sediment is similar to that of LC4 and LC5. Percentage *Calluna* pollen continues to rise until the top of the core where it reaches *c.*75%, whilst levels of *Pinus* pollen fluctuate around 25%. Levels of *Alnus* and *Corylus*-type pollen remain largely unchanged at 1-2%, but there is a notable decrease in the proportion of *Betula* pollen to its lowest level in the profile, occurring at just 1% in samples from the top 8 cm of the profile.

5. East of Faesheallach Burn (FB)

Six zones, FB1-FB6, are described and shown in Fig 5.4e.

East of Loch a'Chnuic

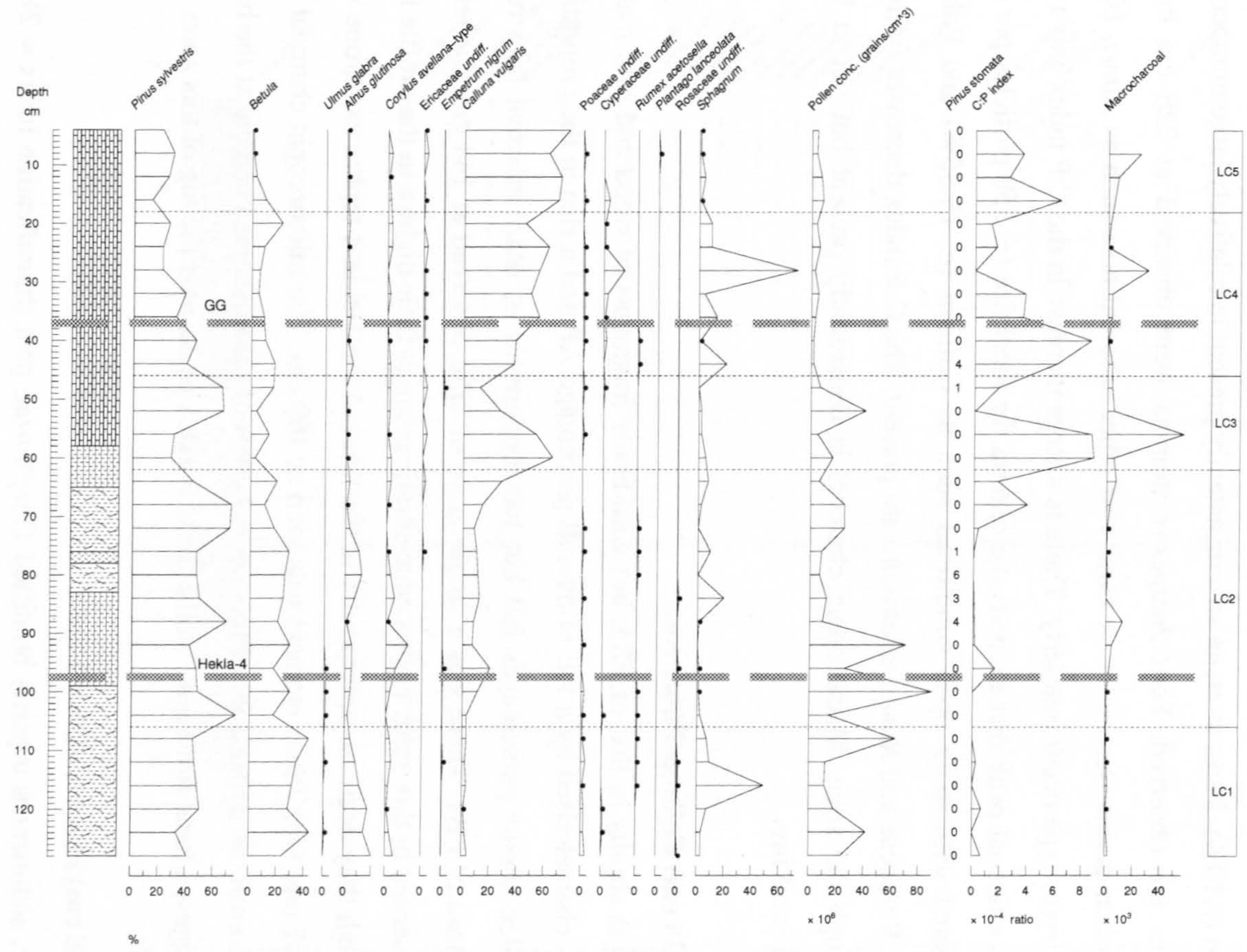


Fig. 6.4d. Summary pollen diagram from east of Loch a'Chnuic, Abernethy Forest. Percentages are based on a Total Land Pollen sum (Total Land Pollen and Spores for *Sphagnum*). For key to stratigraphic symbols see chapter 2. Macroscopic charcoal is measured as particles cm^{-3} in the 150-250 µm size class. Dots represent percentages less than or equal to 1%. The grey dashed lines show the position of the peak concentrations of the Hekla-4 and Glen Garry tephra deposits.

FB1 (232- 184 cm) *Pinus* zone

The basal zone comprises well humified peat with abundant twigs, roots and occasional *Eriophorum* remains (humification index = 2). This zone has the highest percentage AP of the profile, generally around 75-80%, although in two samples the percentage drops to around 60%. The dominant tree pollen taxon is *Pinus* (45-65%), with a steady proportion of *Betula* pollen (*c.*10%). *Pinus* stomata are consistently present in relatively large numbers. No Pinus needles are observed. Four *Juniperus* stomata were observed at 226 cm but no *Juniperus* pollen grains were seen. A variety of other arboreal taxa such as *Alnus*, *Ulmus*, *Salix* and *Corylus*-type occur regularly. There is a large increase in the C:P index and a large macroscopic charcoal peak that exceeds the criteria for local fire (*c.* 550 particles per cm^3). Taxa associated with more open conditions such as *Calluna* (*c.* 15-35%) and Poaceae, Cyperaceae, Rosaceae and *Rumex acetosella* are present. The C:P index decreases from high to low through the zone. Macroscopic charcoal is consistently present but not at levels indicative of local fire.

FB2 (184-138 cm) *Calluna-Pinus* zone

Stratigraphy is similar to that of FB1, but with fewer fragments of wood and root material. This zone is characterised by a fall in overall percentage AP and a rise in the proportion of *Calluna* pollen. *Pinus* percentages fall but the proportions of other arboreal taxa remain similar to those of FB1. There was a single grain of *Tilia* observed at 144 cm. *Rumex* spp. were not observed in this zone. Pollen concentrations are at their highest in the profile in this zone, although they decrease temporarily at the level of the Hekla-4 tephra isochrone which occurs at 152 cm. One *Pinus* stomate was seen at 160 cm. The microscopic charcoal count remains low until the upper limit of this zone. Levels of macroscopic charcoal at the base of the zone suggest a local fire event, whilst the C:P index peaks near the top of this zone.

FB3 (138-88 cm) *Pinus-Calluna* I zone

In this zone, sediment is a partly humified *Eriophorum* peat (humification index = 2), with no woody material or other macrofossils seen. Percentage *Pinus* pollen decreases from *c.* 50% to 40% and percentage *Calluna* pollen increases from 30% to 40%. Pollen concentration also decreases. *Corylus*-type pollen percentages decrease from *c.*10% to *c.*5%, whilst *Alnus* maintains a steady percentage (below 5%). *Pinus* stomata are present at the base of the zone and there is a large peak in both the C:P index and macroscopic charcoal at 112 cm (1224 particles per cm^3), indicating an *in-situ* fire event. NAP pollen occurs frequently at

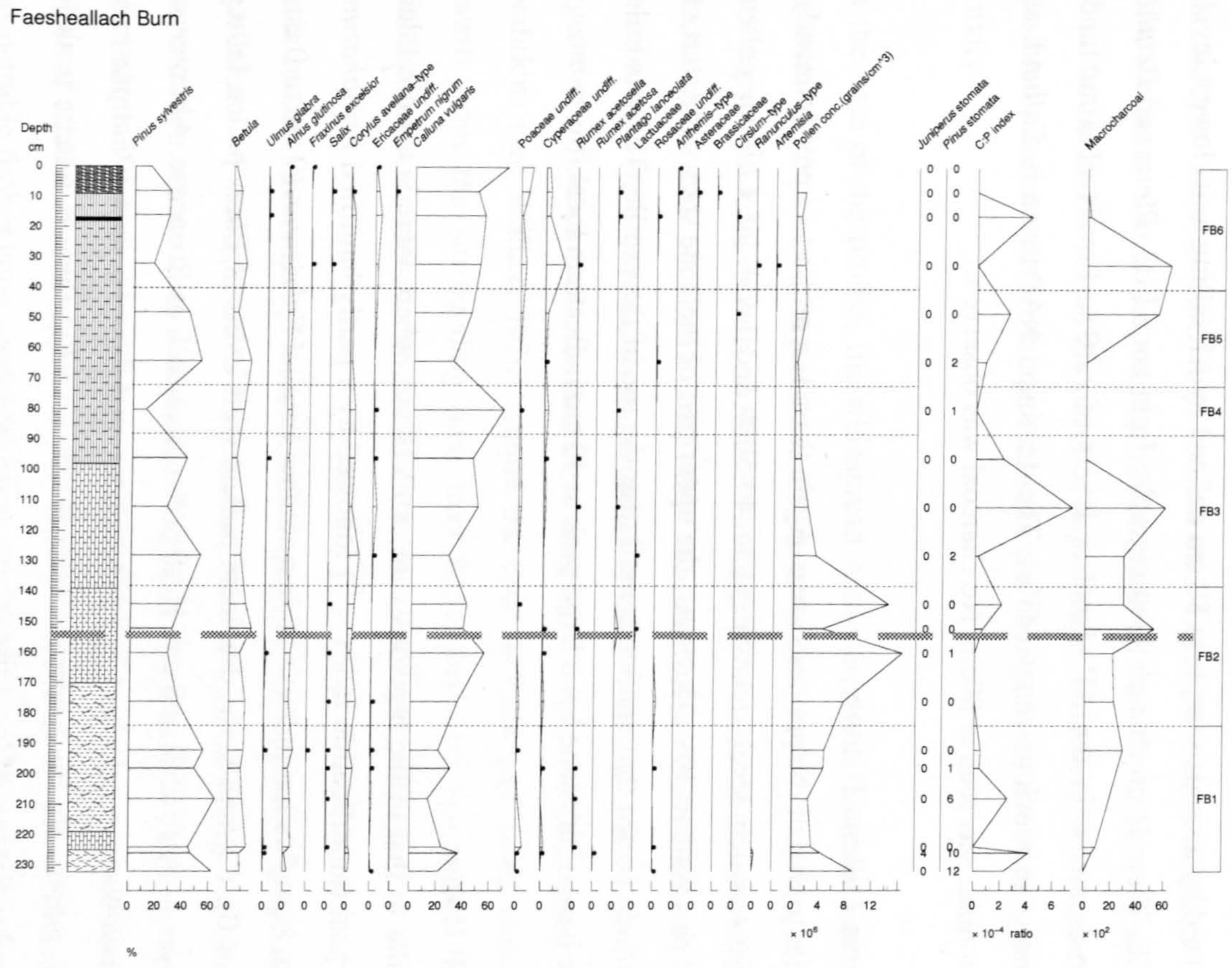


Fig. 6.4e. Summary pollen diagram from east of Faesheallach Burn, Abernethy Forest. Percentages are based on a Total Land Pollen sum. For key to stratigraphic symbols see chapter 2. Macroscopic charcoal is measured as particles cm^{-3} in the 150-250 µm size class. Dots represent percentages less than or equal to 1%. The grey dashed line shows the position of the peak concentration of the Hekla-4 tephra deposit.

low percentages, including Poaceae, Cyperaceae, Rosaceae *undiff.*, *Rumex acetosella* and *Plantago lanceolata.*

FB4 (88-72 cm) NAP I zone

This zone is represented by a single sample at 80 cm defined by AP falling to its lowest level in the profile, at 30%. There is no change in stratigraphy from zone FB3. *Pinus* and *Betula* are more or less co-dominant in the AP signal at levels of *c.*10%. Levels of *Alnus* and *Corylus*-type are similar to previous zones (<5%). The dominant NAP taxon is *Calluna*, at *c.*70%. One *Pinus* stomate was seen at 80cm. No charcoal was observed.

FB5 (72-40 cm) *Pinus-Calluna* II zone

Stratigraphy is similar to that of the previous zone. Again there is a return to a predominantly AP signal, with *Pinus* pollen levels recovering to 40-50% and levels of *Calluna* pollen falling at the start of this zone to 30%. However, the upper part of the zone shows the start of a gradual rise in *Calluna* pollen that continues until near the top of the profile. There is little or no charcoal at the base of the zone but a large peak at 48 cm indicates a local fire event.

FB6 (40-0 cm) NAP II zone

Stratigraphy is similar to that of the previous zone until 18 cm, where there is a 1 cm thick band of *Sphagnum* peat (humification index = 0) followed by a partly humified *Eriophorum* peat (17 cm to 9 cm; humification index = 1) then another band of *Sphagnum* (9 cm to 0 cm; humification index = 0). *Calluna* is the dominant pollen, with levels of *Pinus* pollen falling to 15% at 32 cm, recovering to 25% at 8 cm. Herb pollen taxa such as Rosaceae, Asteraceae, *Cirsium* and *Artemisia* occur regularly at low percentages, and there is a consistent presence of Ericaceae *undiff.* pollen. No microscopic charcoal was seen but there is a large peak in macroscopic charcoal indicative of local fire.

Site development history

1. Tore Hill

Overall, this profile shows relatively few changes, suggesting some degree of long-term homogeneity in the surrounding vegetation and/or the way in which this basin has recorded the pollen signal. However, the possibility of movement of pollen grains cannot be excluded, given the high degree of vertical spread of the tephra in this profile. The main events appear

to be a decrease in the local presence of *Pinus* within the basin that occurred prior to *c.*4600 cal. BP, a marked clearance phase near the top of the profile and a possible increase in the frequency and intensity of regional fire, inferred from the increase in the C:P index towards the top of the profile (Fig. 6.5a). There is no marked change in the long-term pattern of macroscopic charcoal other than at least two local fire events detected in zones TH2 and TH4, the latter also corresponding with a peak in the C:P index. A longer charcoal record would be needed to reveal the onset of any changes in fire regime; from this profile it is not possible to assess whether the pattern seen has changed in a way that is suggestive of human activity.

At the base of the profile, the widespread occurrence of a layer of buried stumps and the presence of *Pinus* wood fragments and stomata in the basal sediments indicate that this basin once supported local growth of *Pinus.* The high percentage of *Pinus* pollen and high pollen concentration are consistent with this inference. Micaceous silty layers overlain by *Phragmites* were recovered from immediately above the stump layer during the preliminary auger survey, which indicates that there may have been a sudden change to wetter climatic conditions (see Walker, 1970) around the time of mass tree death within the basin. Soil inwash from the surrounding area may have produced favourable conditions for the establishment of a reedswamp community (*sensu* Burrows, 1990).

Basin succession continued with the development of a fen community, indicated by the first appearance of recognisable *Eriophorum* remains at 375 cm. A decrease in pollen concentration occurs from this point, which may be a result of both increased rates of basin accumulation (indicated by poorly humified *Eriophorum* peat) and reduced pollen influx due to loss of a local *Pinus* component. Downward movement of pollen with tephra as far as the impenetrable timber layer cannot be excluded, but due to the specific gravity of pollen being lower than that of tephra this seems unlikely. The lack of humification of the sedge peat suggests that accumulation in the basin was now rapid. An apparently temporary decrease in percentage *Pinus* pollen *c.* 4260 cal. BP may correlate with a more regional pine decline. If, however, the signal reflects loss of local *Pinus* from the basin, the increase in the *Betula* pollen signal may have come from trees outside of the basin as pollen source area increased. Opening of the basin is consistent with the occurrence of pollen from *Calluna* and other shade intolerant taxa such as *Filipendula, Plantago lanceolata* and *Rumex acetosella* (zone TH2).

The basin appears to develop with few other changes until the occurrence of a major local fire event near the top of the core (zone TH4), suggested by the large peak in the charcoal record. Bog vegetation may have been destroyed by this event, and vigorous regeneration may have contributed to the subsequent increase of *Calluna* in the pollen record. Alternatively, a large fire may have caused loss or damage of forest trees at a scale sufficient to cause the sudden decrease in *Pinus* pollen seen. Age estimates would be needed to determine whether or not there is any possibility that this fire event matches historical evidence for large fires, such as those of the seventeenth century (Summers, 2005).

Following this fire event, percentages of *Pinus* and *Calluna* pollen return to previous levels, suggesting that disturbance was short-lived. A subsequent decline in *Pinus* pollen may be a result of large scale forest clearance such as occurred west of the River Nethy in the first half of the nineteenth century (O'Sullivan, 1973b). If the series of peaks in microscopic charcoal is interpreted as a regional signal, it appears that fires had already become more frequent, but until this point had not significantly impacted on the vegetation surrounding the basin. At the top of the profile, the increase in *Pinus* and decrease in *Betula* is probably related to recent forestry practices of planting *Pinus* and removing *Betula* (see Summers, 2005).

2. Forest Lodge

A dynamic pattern of basin development and vegetation change is recorded within the sediment from this basin, which discrete tephra layers indicate is largely undisturbed. At the base of the profile, there is a layer of buried tree stumps, located just 6 cm beneath the Hekla-4 isochrone at 194 cm. These may relate to the 'pine decline' of *c.* 4600 cal. BP, where wider climate changes caused conditions in the basin to become too wet for trees. Pollen percentages suggest that *Betula* rather than *Pinus* was the dominant tree species in the surrounding vegetation at this time (Fig. 6.5b). It is unlikely that the basin contained closed forest however, as Poaceae pollen maintains a consistent presence. Low percentages of *Calluna* pollen suggest that heather was not locally present in this part of the forest.

Although *Alnus* is often over-represented in the pollen record due to its high productivity, percentages in excess of 50% in zones FL1 and FL2 almost certainly indicate persistent local presence in the basin itself, possibly colonising from nearby populations in the River Nethy valley. Huntley and Birks (1983) observed that *Alnus* values over 25% commonly occur where *Alnus* is growing within the basin. This may have taken the form of alder carr or a

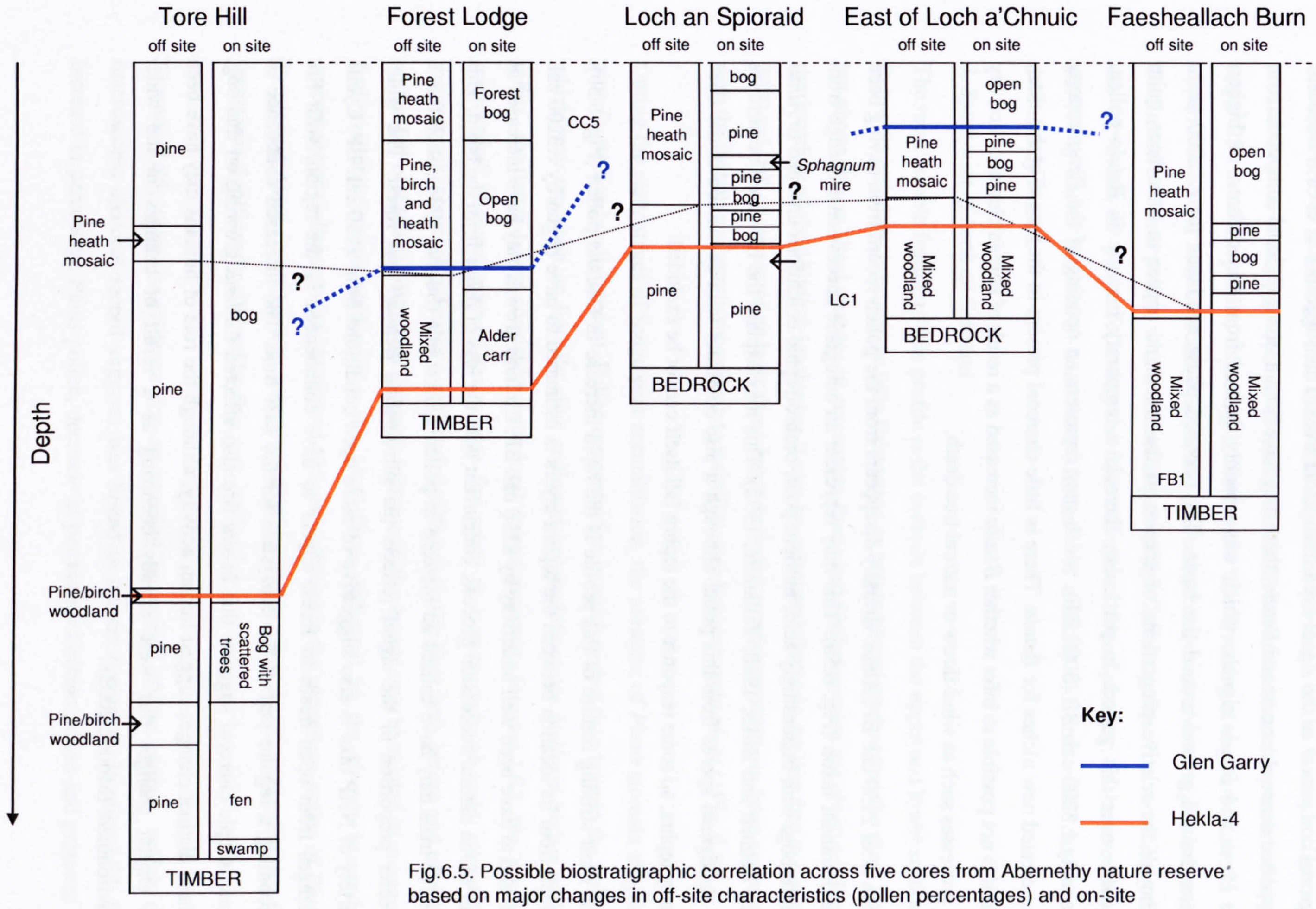


Fig.6.5. Possible biostratigraphic correlation across five cores from Abernethy nature reserve based on major changes in off-site characteristics (pollen percentages) and on-site characteristics (stratigraphy and presence of *Pinus* stomata). The grey dotted line joins depths where the first transition from woodland to heathland was detected. Scales are approximate.

fringe of trees around a wetter central area, possibly including *Betula*. Jackson and Wong (1994) and Jackson and Kearsley (1998) found that the pollen stratigraphy of closed canopy sites could be correlated with that of nearby lakes and bogs, suggesting there is a strong regional component in the signal even from under trees. This suggests that even if the basin supported dense alder carr and *Betula*, there may have been a strong regional component to the *Pinus* and *Betula* signals, which was possibly derived from mixed forest on higher, better-drained ground around the basin. This wooded phase continues for *c.* 2000 years although the relative proportions of species in the woodland appear to have been quite variable over this period. In particular, there is a temporary increase in *Betula* pollen, probably *c.*3200 cal. BP (3000 BP), which may represent an opening of the *Pinus* canopy that created new niches for *Betula*. There is little charcoal present in the record at this time, and it is not possible to infer whether *Betula* increased as a result of human clearance activity or processes such as wind-throw or natural tree death.

Soon after 2150 cal. BP, *Alnus* virtually disappears from the pollen record from having been the dominant taxon (Fig. 6.5b). This may represent an autogenic successional change from fen to bog, with increasingly acid, nutrient poor, ombrotrophic conditions unsuited to *Alnus* (see Bennett and Birks, 1990; Tallantire, 1992). This may explain the increased occurrence of *Sphagnum* spores from this point, although it also coincides with deposition of the Glen Garry tephra, so some response to the tephra fall itself cannot be excluded.

The most striking feature of this profile is the rapid increase in *Calluna* pollen (Fig. 6.5b), which from its location between the tephra layers is estimated to have begun by *c.*3200 cal. BP and to have been well underway by 2150 cal. BP. *Calluna* growth may have increased as part of the natural succession process, concurrent with the loss of *Alnus* from the basin. This loss of trees may have caused an increase in pollen source area (Sugita, 1994), such that a greater proportion of the signal reflects the surrounding *Betula/Pinus* forest. The wider variety of NAP taxa is also suggestive of more open conditions from 2150 cal. BP. Cyclic changes from open heath to forest appear to have commenced in the region, with fire becoming a regular part of the ecosystem for the first time. The increased abundance of macroscopic charcoal suggests that *in-situ* fire also affected *Calluna* growing on this bog. These distinct changes suggest human activity, although the role of humans may have been to exploit changes that were already occurring as a result of changes in the wider environment (Moore, 2000).

Single grains of taxa such as *Tilia*, *Ulmus* and *Quercus* occur until quite recent times and probably represent the long distance component of the pollen signal from a more diverse forest at the regional to extra-regional scale. Certainly for *Tilia*, which occurs at the base of the sequence, it is unlikely that there was any local presence in the Scottish Highlands around the time of the 'pine decline' (Tipping, 2003). Fewer arboreal taxa are recorded in the upper 25 cm of the profile, reflecting a decrease in tree diversity at regional scale. In the uppermost 20 cm, little charcoal is seen, and this corresponds with the AP signal becoming dominated by *Pinus* pollen, with a decline in percentage *Calluna* pollen. It is most likely that this represents the period following the first widespread *Pinus* planting; in the interests of protecting timber production near Forest Lodge it is unlikely this area would have been deliberately burned.

3. South west of Loch an Spioraid

The most notable feature of this profile is the contrast between the upper and lower sections. Below 85 cm, there is relatively little fluctuation in pollen percentages across the main taxa, but above this, cyclical changes in percentage *Pinus* and *Calluna* pollen are observed. From the location of the Hekla-4 isochrone, it can be estimated that this cycling began around 3200 cal. BP. A series of at least three heath-to-forest transitions seems to have occurred, with the system apparently recovering to a similar state between open phases (Fig. 6.4c).

During the early stages of sedge peat accumulation, the presence of *Pinus* stomata suggests pine forest was locally present. Pollen concentration is much higher than later in the profile, which may represent an initially slow sediment accumulation rate and/or a higher pollen influx, the latter being consistent with local *Pinus* presence. In zone LS2, the peak in microscopic charcoal may reflect a large fire event at a more regional scale, whilst the macroscopic charcoal indicates a phase of significant *in-situ* fires both before and after the tephra fall of 4260 cal. BP. This apparent increase in fire events may be related to increased fuel availability associated with a rise in *Calluna*, indicated by the already increasing percentage of *Calluna* pollen. At around 116 cm, a decline in the percentage pollen of *Pinus*, *Betula* and *Alnus* coincides with a large peak in the regional fire signal, suggesting that the forest was significantly affected by fire.

In zone LS3, there is evidence for an opening or retreat of the canopy, which the macroscopic charcoal record suggests was linked to a local fire event. In zone LS4, the increase in percentage *Pinus* pollen, decrease in percentage *Calluna* pollen and presence of

Pinus stomata suggest that forest cover extended once again over this site. An increase in the C:P index may represent a higher regional charcoal component, related to a more intense fire regime during this period. Zone LS6 appears to represent a change back to locally present *Pinus* with *Calluna* for a third time, which again is supported by the presence of *Pinus* stomata.

In the context of the longer sequence *Betula* pollen does not appear to have fluctuated much above the 10% level, and probably remained relatively unchanged until recent times. The pollen assemblage of zone LS7 suggests an open heath and, from the profile of macroscopic charcoal, it appears that local fire was frequent throughout this period as in previous NAP zones. The decrease in the C:P index in zone LS8 suggests a general decline in regional fire events in the recent past, and the small amounts of macroscopic charcoal recorded in this zone also suggest that *in-situ* fire also occurred less often, possibly related to fire suppression close to the forest edge.

4. East of Loch a'Chnuic

The Hekla-4 tephra layer occurs near the base of the profile (Fig. 6.4d), suggesting that active sediment accumulation only began mid-way through the Holocene (estimated at 5700 cal. BP or 5000 BP). *Pinus* and *Betula* appear to have been the dominant taxa at this time, and the presence of woody detritus at and near the base of this profile indicate that this site once supported tree growth. The consistently high proportion of AP in the lower half of the profile suggests that there was little change in the degree of forest cover until around 3200 cal. BP (3000 BP). The consistent occurrence of Poaceae and other shade intolerant taxa such as *Rumex acetosella* suggests at least a partly open canopy.

Several changes are observed for the period around 3200 cal. BP. A decrease in percentage *Alnus* pollen may reflect coppicing or clearance by humans. Alternatively, natural processes of river down-cutting and erosion in the adjacent River Nethy valley could have led to loss of suitable substrate. This is consistent with the relatively high mineral content of the sediment in this core, which may be the result of eroded material having been transported into the basin by wind or floodwater. The presence of woody layers and *Pinus* stomata indicate local presence of *Pinus* prior to 3200 cal. BP. After then, *Calluna* began to replace *Pinus* as the dominant pollen taxon and the charcoal record suggests an increased frequency of fire events at both local and regional scales. By zone LC4, *Pinus* pollen percentages increase and stomata are again observed, suggesting recovery of *Pinus* forest and providing

evidence for two successive forest-heath transitions, similar to those seen south of Loch an Spioraid. From then on, the steady increase in the proportion of *Calluna* pollen implies an increasingly open landscape maintained by, or cleared for, grazing.

5. East of Faesheallach Burn

The profile from this site (Fig. 6.4e) is similar to that of site LC, which is located 1 km to the north east of site FB. This suggests that the local and regional changes recorded were similar across this part of the reserve. Having initially supported tree cover, the area shows subsequent signs of at least three cycles of forest opening and recovery in the period following 4260 cal. BP, with a final downward trend in the proportion of AP, levelling out within the top 30 cm of the profile. It is possible that the recovery of tree growth was hampered by a progressive increase in *Calluna*, although this increase is not so pronounced as in the Loch a'Chnuic profile. The regional charcoal signal suggests a similar change in fire regime, with regional fire events appearing to increase after around 3200 cal. BP. The scarcity or absence of macroscopic and microscopic charcoal and decrease in percentage *Pinus* pollen around zone FB5 suggests a sustained period where fire activity decreased. This may represent a decrease in human fire activity, possibly associated with a wet phase in the climate such as that of *c.* 2700 cal. BP (2500 BP) detected at Tore Hill by Blundell and Barber (2005). In the top 30 cm of the core, there is relatively little change in the pollen profile, suggesting that open *Calluna* heath has existed here for several hundred years. As with the other profiles, the inferred recent increase in *Pinus* probably reflects tree planting and, latterly, encouragement of natural regeneration.

Discussion

It is apparent that the five sequences presented here differ from each other in many respects. For much of the time they probably recorded mainly local, rather than regional, changes, although the two blanket bog sites LC and FB probably reflect more regional vegetation since becoming more open. This makes correlation with existing regional profiles from the area difficult, particularly as the shorter time spans covered by these profiles means that events are detected at finer temporal scales. Radiocarbon age estimates would be particularly useful for dating major changes, *e.g.* the onset of heathland development and the timing of forest to heath transitions, which occur at sites LS, LC and FB (Fig 6.6). In addition, it would be useful to obtain further samples from either side of peak maxima or minima that are

currently represented by a single pollen sample, *e.g.* zones TH4 and LC2, as recommended by Faegri and Iverson (1989).

Pine decline

Several theories attempt to explain the 'pine decline' of *c.*4600 cal. BP, which are discussed in chapter 1. One idea is that it is related to the Hekla-4 tephra deposition (*e.g.* Blackford *et al.*, 1992). Langdon and Barber (2004) examined Hekla-4 tephra deposits from all over Scotland and found variable levels of deposition, therefore linking tephra deposition to the Scotland-wide climate changes implied by the 'pine decline' may not be justifiable (Whittington and Edwards, 1997). At Abernethy nature reserve, high shard concentrations were found at Mallachie Moss near Loch Garten. It may be that the Hekla-4 tephra deposit was of sufficient magnitude to be damaging to vegetation in parts of the reserve.

At sites TH, FL and FB, the presence of numerous tree stumps at the base of the recovered sediment suggests that a series of changes sufficient to cause mass tree death has occurred. Only in one site (FL) does this date from *c.* 4600 cal. BP. At the other two sites, the location of Hekla-4 tephra layer suggests a much earlier date (assuming the presumed location of the tephra layer at site TH is correct). Pollen evidence for a pine decline from these profiles is inconclusive. A slight decline in percentage *Pinus* pollen is seen at TH, but for sites LC, LS and FB there is little or no change in the pollen record at the time of the Hekla-4 tephra fall. However, at FL, the pollen signal shows a rapid but temporary decrease in both pollen concentration and pollen percentage of the dominant tree species (*Betula*). A tentative explanation for this is that variable rainout of tephra affected some areas more severely than others (see Dugmore *et al.*, 1995), and that this was sufficient to impede tree growth and/or pollen production for many decades.

The idea of local variations in tephra distribution across the reserve is supported by the failure to detect the Glen Garry tephra layer at all sites, despite careful searching. There is pollen and dendrochronological evidence for tephra falls having caused tree death (*e.g.* LaMarche and Hirschboek, 1984; Baillie and Munro, 1988), including *Pinus* in the north of Scotland (Blackford *et al.*, 1992). However, Hall *et al.* (1994) found no correlation between a decline in *Pinus* pollen and the Hekla-4 eruption in Ireland, suggesting that toxic effects or climatic deteriorations after such eruptions do vary geographically. The possibility of smaller scale variations in tephra effects within the reserve cannot be excluded, but higher resolution sampling would be needed to study this further.

Forest composition

In all sites, it appears that forest composition remained largely unchanged prior to 3200 cal. BP. The area around Forest Lodge appears to have supported much more mixed woodland than the other sites. Although the overall percentage AP declined with the rise in *Calluna* around 3200 cal. BP, diversity appears to have been maintained for at least another 900 years. *Alnus* appears to have irreversibly declined around 2150 cal. BP, although its decline in the pollen record may be partially accounted for by the practice of coppicing and, latterly, by removal from areas suitable for forestry. Likewise, *Betula* has all but disappeared from the pollen signal for the section of profile representing the past few hundred years, probably related to preferential planting of *Pinus* as a timber crop.

Corylus-type pollen occurs in all sites at consistently low percentages. Assuming the pollen is *Corylus* and not *Myrica*, this may be more a reflection of its manipulation by coppicing than its scarcity. Alternatively, flowering may not have been significantly suppressed if hazelnuts were important as a food source. It may be that *Corylus* did not remain an important woodland component once *Pinus* had risen to dominance, or occurred locally in pockets not detected by this scale of study.

Heathland development

Heathland appears to have first developed in the higher altitude, more exposed parts of the south and east of the study area. The marked increase in *Calluna* recorded by the pollen profiles across four of the five sites appears to have occurred first at site FB, possibly between 5700 and 5100 cal. BP (5000-4500 BP). This is the most exposed, highest altitude site (450 m asl) and the increase here is less pronounced than at the other sites, as *Calluna* was probably already present in larger amounts within a less dense forest closer to its altitudinal limit. At site TH, there is a small increase in *Calluna* pollen that appears to pre-date the arrival of *Alnus* but the consistency of the *Calluna* pollen percentage throughout most of this profile suggests that this is a local signal from a relatively undisturbed raised bog surface rather than a reflection of heathland development in the wider landscape.

From the location of these changes relative to the tephra layers (Fig 6.6), it appears that the rise to dominance of *Calluna* began around 3200 cal. BP at the other three sites, manifesting slightly differently in the pollen record depending on the characteristics of the surrounding vegetation. The longer term, regional context provided by the sequences in chapter 5 suggests that this was actually a second major cycle of *Calluna* expansion and decline, with

the first decline having occurred by *c.* 6400 cal. BP (5500 BP) as seen at North Abernethy (chapter 5, Fig. 5.6). The second phase of *Calluna* expansion differs from the first in that it coincides with an unprecedented decrease in AP, suggesting that additional factors, such as increased forest clearance by humans, were also in operation.

There is evidence to suggest that recent heathland-forest transitions have taken place at LS, LC and FB (Fig. 6.5). At LS, the top 50 cm closely resembles O'Sullivan's (1973a) Loch an Spioraid sequence, which was recovered from 100 m due east of LS. O'Sullivan interpreted this as a record of at least two successive encroachments of closed pine forest upon heathland, the most recent having occurred at AD 1870. The new profile from LS seems to have recorded the same sequence of events, and the longer-term context suggests that the shift from pine forest to open heath back to pine forest has occurred here at least three times since *c.* 3200 cal. BP. The pollen and charcoal records indicate that an increase in *Calluna* broadly corresponded with the occurrence of *in-situ* fire, as observed by Odgaard (1992).

This cycling may reflect advance and retreat of the position of the forest edge across the site, which is supported by the observation that *Pinus* stomata were only observed during the phases where *Pinus* pollen increases. Fifty metres south of the site, there is an area of the forest that has been continuously wooded since at least 1750 (O'Sullivan, 1973b; Summers, 2005), which may have acted as a refuge and seed source to facilitate *Pinus* regeneration. It is likely that human use of fire was directed at forest edges rather than within the forest, as edges would have been more accessible and acted as firebreaks. The location of site LS near to relatively low-lying, flat terrain close to Loch an Spioraid and the River Nethy may have made it an attractive area for settlement and grazing, sheltered to the east and south by the Braes of Abernethy and the Cairngorms.

In the LC profile, following the initial increase in percentage *Pinus* pollen, there appear to be three similar heath to forest transitions prior to a downward trend in the percentage AP. From *c.*3200 cal. BP, there is a dramatic increase in percentage *Calluna* pollen, followed a sharp decline and recovery by 2150 cal. BP. From then on, percentage *Calluna* pollen progressively increases to its present high levels. Before *c.*2150 cal. BP, it appears that *Pinus* could regenerate to previous levels, but once *Calluna* began to colonise formerly forested areas, tree regeneration was progressively inhibited, possibly as a result of repeated burning or sustained grazing.

This fits with Gimingham's (1972) argument that early transitions to heathland were reversible, but if they are to be maintained indefinitely some factor or combination of factors must prevent the return of shrubs and trees. However, the role and relative importance of such factors can be difficult to establish. In an attempt to explore the effects of over-burning on *Calluna* using pollen and charcoal records, Stevenson and Rhodes (2000) were unable to separate the possible effects of fire from those of grazing. This indicates that where both fire and grazing are thought to have operated alongside other factors, care is needed when studying heathland development using palaeoecological records.

Fire history and human activity

The role of fire appears to have varied between sites, with TH showing some peaks in the regional burning signal from around 3200 cal. BP, corresponding well with indicators of increased *Calluna* (*cf.* Odgaard, 1992). For FL, the charcoal records suggests minimal occurrence of local fire. This site also does not appear to have recorded variations in regional burning, which may be related to the more local collecting properties of this basin. The most striking change in the pattern of microscopic and macroscopic charcoal is seen at LC. Here, there is a sudden change from almost no charcoal in the samples from the lower half of the profile to a record indicative of cycles of increased regional burning, the peaks of which correspond with periods of increased *Calluna* pollen. This is interpreted as a change from a 'natural' fire regime to a human-induced one, with increased frequency and continuity in the charcoal record. During this phase, which appears to start *c.* 3200 cal. BP and continue until the recent past, the macroscopic charcoal record is also consistent with increased occurrence of local fires.

Before the onset of the heathland cycling inferred at site LS, the pollen record suggests closed pine forest, during which there is one pre-Hekla-4 phase where *Calluna* appears to increase during a period of more intense regional and local burning. At around 4260 cal. BP, the *Calluna* pollen percentage begins to decrease, and there is little subsequent evidence for local or regional fire until the onset of the heathland cycling. As this earlier period of increased fire events is not associated with the onset of cyclic heath to forest transitions seen in the upper zones of the profile, it seems unlikely that increased fire alone was sufficient to change the system.

The change to a cyclic pattern of heath and forest probably also involved an increase in grazing which suppressed regeneration of *Pinus*, some time after environmental changes

associated with the decline in tree growth *c.* 4600 cal. BP. This lends support to the idea of a 'least effort scenario' discussed by Moore (2000), where increased frequency of environmental disturbance events such as wetter conditions and/or tephra deposition allowed manipulation of the forest through fire on an opportunistic basis. A higher resolution analysis of pollen and charcoal would allow further assessment of the relationships between fire events and *Calluna* loss/regeneration.

Conclusion

There is no conclusive evidence for the mid-Holocene 'pine decline' at Abernethy Forest, but two of the five sites studied show some evidence of temporary changes that be related to the Hekla-4 tephra deposition. The sequences presented here show that forest composition was locally variable across the reserve. Temporary heathland formation seems to have begun at higher altitudes in the south of the study area as early as 5700 cal. BP (5000 BP). There was a slight increase in *Betula* around this time which may have been related to temporary anthropogenic clearances, but otherwise little change in forest composition occurred before 3200 cal. BP, from whence there is a rise in percentage *Calluna* pollen in all profiles, and a gradual decline in forest cover. This marks the start of heathland development across much of the reserve. Human-induced fire appears to affect vegetation development in cycles lasting several hundred years that may have been modulated by wet shifts in the climate. These results support the idea that the first widespread, and, arguably, progressively irreversible, impact of humans on the Abernethy landscape began around 3200 cal. BP in the late Bronze Age /early Iron Age.

In chapter 7, the palaeoecological records from all seven cores will be compared and fossil pollen assemblages from three time slices will be used to reconstruct the landscape to provide further insight into heathland dynamics and changes in forest composition since 6400 cal. BP (5500 BP).

Chapter 7. Reconstructing past vegetation in Abernethy Forest using a modelling approach

Introduction

Chapter 4 demonstrates that models of pollen dispersal and deposition can be successfully used to simulate modern pollen rain for the major taxa and land cover types within present-day Caledonian pine forest landscapes. This chapter shows how such models can be applied to the reconstruction of past vegetation in such landscapes, using palaeoecological data from chapters 5 and 6. Landscape reconstruction has long presented challenges for palaeoecologists (Sugita, 1994), but an important initial stage is to establish in a more quantitative way how fossil assemblages reflect the surrounding vegetation. Evidence from recent studies using the Prentice-Sugita model (Prentice, 1985; Sugita, 1993, 1994) for simulating modern pollen rain in Scandinavian cultural landscapes (*e.g.* Broström, 2002; Nielsen, 2003; Broström *et al.*, 2005) suggest that many of the basic mechanisms of pollen dispersal can be modelled sufficiently well to justify the incorporation of such models into the reconstruction process.

The ERV model was initially published with an inverse form to provide a means of calculating vegetation data from fossil pollen samples (Parsons and Prentice, 1983). However, the output for inverse ERV takes the form of distance-weighted plant abundance (DWPA), which does not have the spatial properties that are required for producing spatial maps of past vegetation. If a network of sites with overlapping relevant source areas of pollen (RSAPs) is available, cross-checking of any inferences made about the distribution pattern of major vegetation types should be possible. Adjacent sites producing similar pollen signals would suggest that a larger patch of a particular vegetation type extended across the area enclosed by the RSAPs. Alternatively, adjacent sites with marked differences in their pollen signals would suggest changes in vegetation type at a scale detectable by the RSAPs of sites straddling the transition between one vegetation type and another. Spatial reconstruction could be refined further using geophysical characteristics of the landscape to constrain the possible distribution of plant communities, *e.g.* data on geology, soils and topography.

The Multiple Scenario Approach

An alternative approach is to start from understanding of plant autecology and use this to advance hypotheses that can be used to generate possible past landscape scenarios. Pollen

dispersal modelling now provides a means of testing such scenarios more objectively than has previously been possible (*e.g.* Caseldine and Fyfe, 2006). In what is essentially the same modelling process used in chapter 4, pollen loading is simulated for each possible landscape scenario to obtain simulated pollen assemblages for sample locations corresponding to coring sites. These are then compared with the fossil pollen assemblages and the landscapes producing simulated pollen assemblages most similar to the fossil assemblages are identified as the most feasible landscape scenarios. This is known as the Multiple Scenario Approach (MSA) (Bunting *et al.*, accepted).

Scenario creation

The first stage of the MSA involves using the palaeoecological record to identify the main plant taxa likely to have been present in the region. Many possible scenarios for the distribution of those taxa can then be created, using ecological restraining rules based on knowledge of plant autecology combined with properties of the physical environment such as altitude, aspect, geology or soil type, wetness and slope (Bunting *et al.*, submitted).

A potential problem with scenario creation based on existing ideas about past vegetation is that subjective judgements about how a past landscape may have looked could unduly influence scenario creation. One way to minimise this subjectivity is to use a 'fuzzy decision making' process, first conceptualised by Zadeh (1964), which enables subjective concepts to be dealt with in a rational way. Objectivity can be achieved by using a model of the physical landscape upon which replicable rules or procedures are operated.

A digital elevation model (DEM) is used as a basis for the addition of data layers containing other information, *e.g.* water features. This provides a means of including many features of the landscape that are likely to have been persistent over palaeoecological time (e.g. slope, altitude, aspect). If it is assumed that abiotic features such as geology, topography and the locations of water features for inland landscapes are not likely to have changed greatly over the past 5000 years, modern day features can be used as a basis for generating past landscape scenarios.

The PC programme LANDSCAPE (Middleton and Bunting, in prep.) is designed for scenario generation and manipulation of grids of real and categorical information. It allows ecological restraining rules to be applied to grids containing information on the physical features of the landscape as described above. Rules can be applied with varying user-defined

probabilities *e.g.* 'if altitude > 650 m (> 800 m), probability of community A is 100% (75%, 50%); randomly place patches of community B to (25%, 50%) of cover if within (25 m, 50 m) of water. This maintains a replicable procedure for a given set of rules (Middleton and Bunting, in prep.). The fact that the eventual outcome (*i.e.* most feasible scenario) is unknown at the outset and is eventually decided by statistical comparison of simulated pollen assemblages with the fossil pollen assemblage minimises the opportunity for subjective judgements about the characteristics of a past landscape.

Simulation of pollen assemblages

Pollen assemblages are simulated using the Prentice-Sugita (Prentice, 1985; Sugita 1993, 1994) model of pollen dispersal and deposition (see chapter 4). This can be carried out using PolFlow (Bunting and Middleton, 2005) or its unpublished variant POLLEN which can process a large number of scenarios at a time. Input parameters required as the same as those used in chapter 4, *i.e.* relative pollen productivity and pollen fall speeds for each taxon.

Identification of most feasible landscape scenarios

Once all the simulated pollen assemblages have been obtained for each core site, the most feasible landscape scenario is selected by statistically comparing the simulated pollen assemblages with the fossil assemblages to determine the 'best fit'. This is determined numerically using dissimilarity coefficients to calculate the degree of similarity between simulated and fossil pollen. Landscapes which produce pollen assemblages most similar to the fossil assemblages (*i.e.* the smallest dissimilarity coefficients) are identified as the most feasible.

The MSA was adopted for several reasons. Firstly, for major Caledonian pine forest tree taxa, plant autecology is generally well-studied (*e.g.* Grime *et al.*, 1988; Chambers and Elliot, 1989; Tallantire, 1992; Huntley, 1993). There are a number of hypotheses concerning the types of processes and long-term vegetation changes that have affected the landscape, albeit at a general scale (*e.g.* Bennett, 1984, 1996; Birks, 1989), *e.g.* that the *Pinus* tree line reached at least 790 m by *c.* 5500- 4400 cal. BP (5000- 4000 BP; Dubois and Ferguson, 1985; Bennett, 1996); or that heathland development became widespread after *c.* 3200 cal. BP (3000 BP; O'Sullivan, 1974, 1976). Until recently, opportunities for testing such hypotheses have been limited, as past landscape reconstructions could not be tested against fossil pollen data with the same degree of objectivity afforded by the MSA.

Secondly, reconstruction of the distribution and composition of vegetation mosaics is still difficult using pollen analysis alone because of the complex taphonomy of pollen and the problems of understanding pollen source areas in semi-open landscapes. As was the case in this study, macrofossil may not be available to provide additional information on local plant presence and, in some cases, the availability of suitable sediments in the desired sampling locations may be limited (Bunting *et al.*, submitted). For studies involving a network of sites, the limited availability of sites may mean that estimated relevant source areas of pollen do not overlap, which makes reconstruction using inverse ERV and DWPA difficult.

Although in its early stages of development, the MSA offers real scope for testing hypotheses about vegetation change and improving landscape reconstructions. So far it has been used to explore the extent and character of open areas in disturbed woodland in central Ireland at the time of the elm decline and Neolithic agricultural clearances (Caseldine and Fyfe, 2006), to reconstruct a cultural landscape in north west Scotland (Bunting *et al.*, accepted) and to reconstruct the position of the mid-Holocene tree line in the Peak District (Bunting *et al.*, submitted).

Aims

The aims of this chapter are to i) test hypotheses concerning processes of vegetation change for Caledonian pine forest using the Multiple Scenario Approach; ii) produce feasible landscape reconstructions for three past time slices; iii) propose a conceptual model of long-term vegetation change in the Abernethy landscape over the last 6400 years

For i), evidence from the seven cores presented in chapters 5 and 6 are combined with existing theories of landscape change and knowledge of plant autecology to advance hypotheses relating to major processes of change such as climate change, fire regime and human activity. These are then tested using the MSA. In ii), the most feasible scenarios for 6400 cal. BP (5500 BP), 4260 cal. BP (3830 BP) and 2150 cal. BP (2100 BP) are identified and presented as 'palaeo maps' alongside a similar map for present day land cover. For iii), mechanisms for long-term landscape evolution that may have given rise to these 'snapshots in time' are identified, using inferences from the profiles analysed in chapters 5 and 6.

Hypothesis generation

For the period following the initial post-glacial colonisation of major taxa but prior to major human impact, ecological factors (*e.g.* relating to climate, soils, topography and competition)

would have been major influences on woodland composition, expansion and distribution (Birks, 1989). It should therefore be possible to base scenarios on plant ecological preferences for the period prior to human influence. *Alnus* favours wet, mildly basic habitats such as riversides, fens and floodplains (Bennett and Birks, 1990) below 300 m, whilst *Betula* can tolerate more acid conditions and is a colonist of burnt areas, open ground and forest clearance (Grime et. al, 1988). *Pinus* often occurs as a dominant forest tree, but on good soils it is a poor competitor with deciduous tree species such as *Quercus* and Ulmus and is less able than *Betula* to invade gaps (Bennett, 1984).

Whilst it cannot be certain that the ecological preferences of the plant taxa and communities being modelled have not changed since the mid-Holocene due to a lack of modern analogue communities, for the purposes of these reconstructions it will be assumed from uniformitarian principles that they behaved in a similar manner to their modern counterparts. Modelling of processes involving human activity is difficult, as complex and poorly understood human impacts on the landscape have led to changes in plant communities, including the emergence of new ones (Birks, 1986). A simpler approach is to represent processes through their likely effect on the landscape, *i.e.* in terms of how they may have affected vegetation patterns. A wide range of vegetation patterns can then be tested against fossil pollen data using pollen dispersal modelling.

Study area

The study area was the same 15 km x 15 km square used for the simulations in chapter 4. Core locations are shown in relation to the DEM in Fig. 7.1.

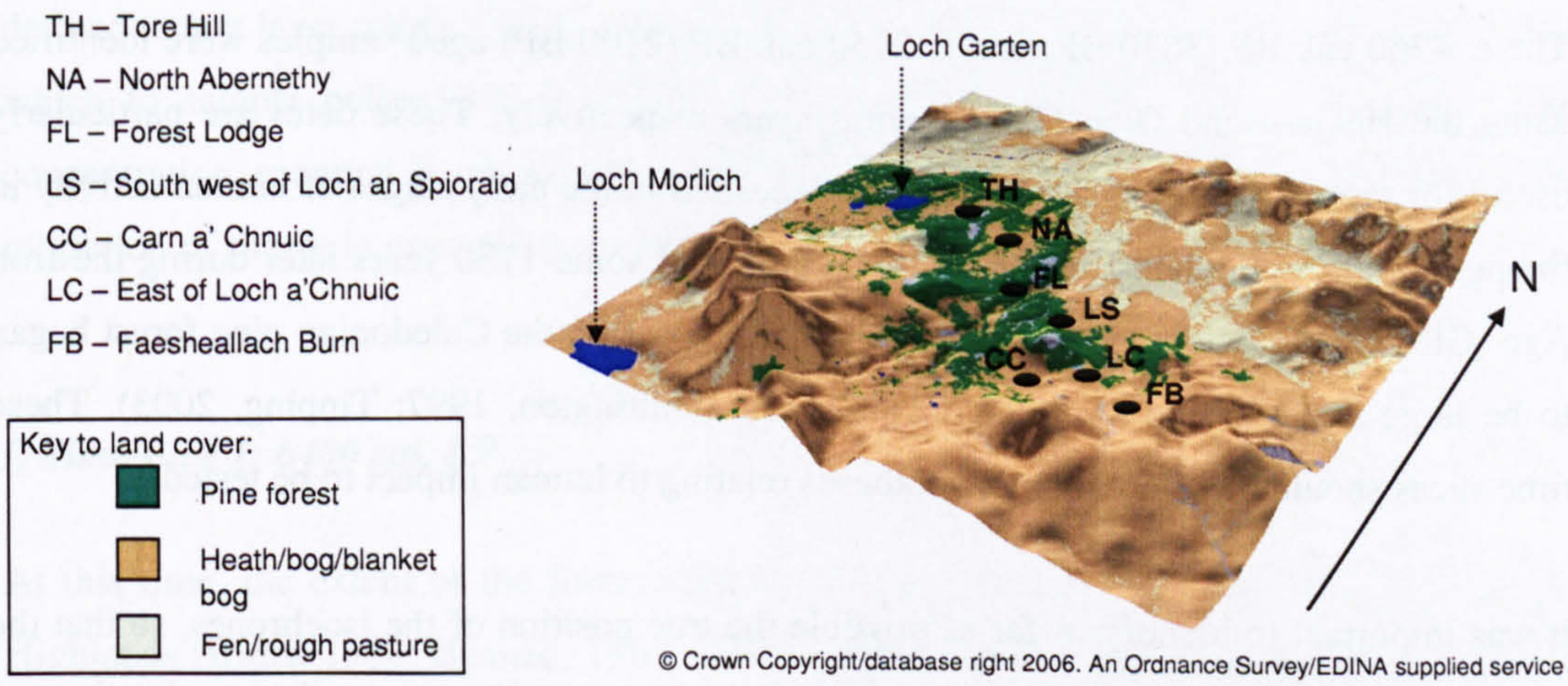


Fig. 7.1. Digital elevation model for the 15 km x 15 km study area at Abernethy nature reserve, showing locations of core sites.

Identification of time slices

Age estimates have previously been published for readily identifiable changes in pollen records from the region. In the absence of an age-depth model, such changes can be used as biostratigraphic markers to obtain pollen data for testing possible landscape scenarios for the period prior to significant human impact. It was also intended that this time slice would act as a basis for modification when applying restraining rules relating to subsequent landscape changes. A suitable marker is where percentage *Alnus* pollen increases to more than 4%, which O'Sullivan (1974a) suggests marks its expansion in the Abernethy area. This event has been dated by Birks and Mathewes (1978) to *c.* 6400 cal. BP. The three cores in which this event was observed were Tore Hill (TH), North Abernethy (NA) and Carn a'Chnuic (CC), so it was estimated that these sections of the cores would provide pollen assemblages from *c.*6400 cal. BP.

The time slice was located at the point of the first pollen sample where *Alnus* pollen proportions reached at least 4%, at or shortly after the first maximum in percentage *Pinus* pollen. Although there are problems with tephra dispersal in two of these cores (see discussion in chapter 5), it was assumed that pollen had not been disturbed to the same degree as tephra. Birks and Birks (1980) point out that the vertical mixing of pollen in peat sediments is not generally important within the time scales involved in most pollen studies. The pollen assemblages were therefore considered suitable for locating the increase in percentage *Alnus* pollen for what was in any case an approximation exercise. The similarity between the pollen assemblages across the cores at this time suggests they were all reflecting the same expansion of *Alnus* at the regional scale.

The *c.* 4260 cal. BP (3830 BP) and *c.* 2150 cal. BP (2100 BP) aged samples were identified using the Hekla-4 and Glen Garry tephra layers respectively. These dates are particularly useful for reconstruction as the tephra was deposited in the early stages of human activity in the region during the late Bronze Age (Hekla-4) and some 1730 years later during the Iron Age (Glen Garry) when it is argued that human impact on the Caledonian pine forest began to be large scale and destructive (Edwards and Whittington, 1997; Tipping, 2003). These time slices should therefore allow hypotheses relating to human impact to be tested.

It was important to identify as far as possible the true position of the isochrones, so that the pollen sample used was the best representation of surrounding vegetation at the time of tephra deposition. Although it was possible to characterise Hekla-4 tephra from all seven

cores from Abernethy Forest based on reference tephras (Dugmore, 1989; Dugmore *et al.*, 1995; see chapters 5 and 6), it was only possible to locate the isochrone itself in five of the seven cores for reconstruction of the 4260 cal. BP time slice: FL, Loch an Spioraid (LS), NA, Loch a'Chnuic (LC) and Faesheallach Burn (FB). In cores TH and CC, the vertical dispersal of Hekla-4 shards was considered too great to allow identification of the isochrone (Chapters 5 and 6; Fig. 7.2).

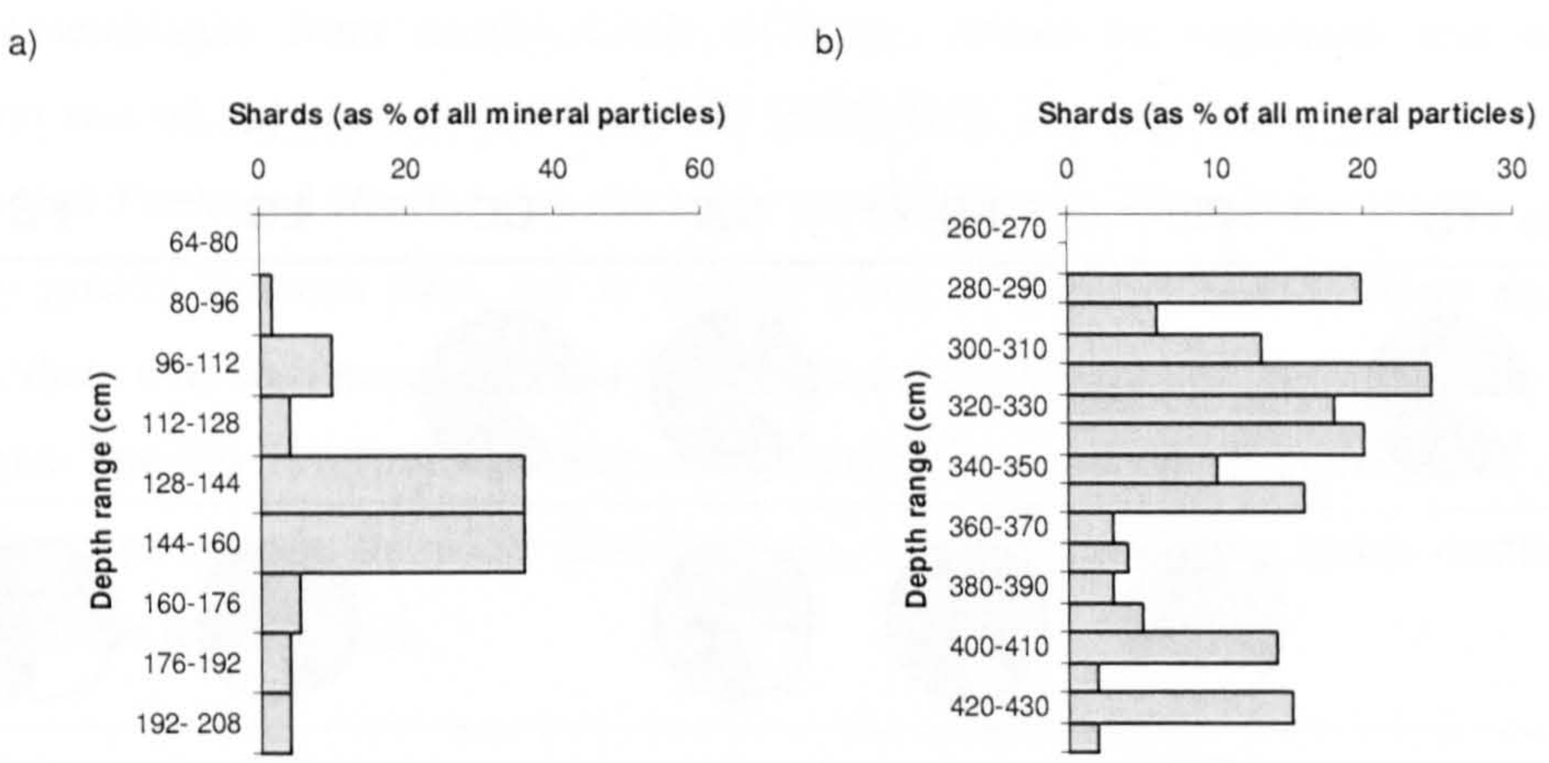


Fig. 7.2. Vertical distribution of Hekla-4 tephra shards in cores from Carn a'Chnuic (a) and Tore Hill (b), showing evidence of upward and downward dispersal (Carn a'Chnuic) and a long but irregular downward tail (Tore Hill).

In the other five cores with Hekla-4 tephra and the two cores with Glen Garry tephra, appropriately aged samples were relatively easy to locate, as there was a discrete, well-defined tephra layer which peaked within 1-2 cm depth. Selecting the appropriate depth from which to sample pollen was therefore relatively straightforward. Where the peak shard concentration spanned 2 cm depth, the uppermost depth was selected on the basis that migration of shards is more likely to be downwards by gravity.

i) Time slice 1: 6400 cal. BP

At this time, the extent of the forest appears to have been at its maximum in the Scottish Highlands (Birks, 1988; Bennett, 1984, 1995, 1996; Tipping, 1994), with the *Pinus* tree line in the Cairngorms estimated at 880 m (Huntley *et al.*, 1997). This suggests that there was considerable open habitat at higher altitudes (MacKenzie, 2002). In the Cairngorms region,

Tipping (1994) suggested that a mosaic of different stand types probably existed, with *Betula*, *Pinus* and *Alnus* co-existing at lower altitudes. Alternatively, MacKenzie (2002) suggests that *Alnus* woodland dominated the more fertile alluvial soils of Strathspey but it also extended to 400 m altitude (Birks, 1989). It is likely that there were openings in the forest canopy, caused by animal activity (*e.g.* boar and beaver), tree disease and death, lightning strikes, fire and wind-throw (Edwards and Whittington, 1997). Blanket bog was probably not extensive at this time (Mackenzie, 2002), and human activity was probably had a minimal overall impact on the landscape (Edwards and Whittington, 1997; Mackenzie, 2002).

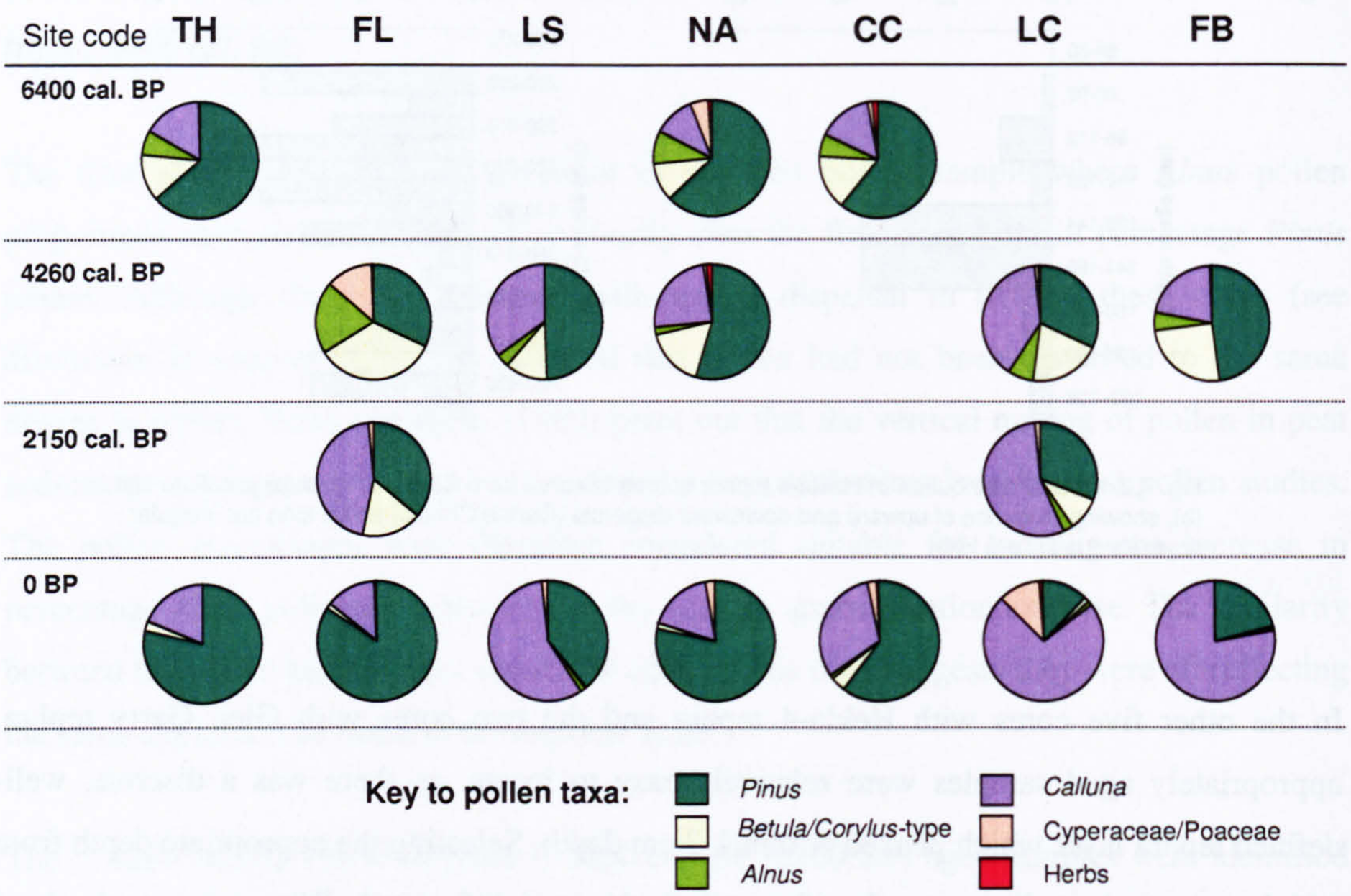


Fig. 7.3. Pollen proportional data used for reconstruction of each time slice. Site codes: TH (Tore Hill), FL (Forest Lodge), LS (Loch an Spioraid), NA (North Abernethy), CC (Carn a'Chnuic), LC (Loch a'Chnuic), FB (Faesheallach Burn).

Comparison of pollen assemblages between sites

For this time slice, three cores (TH, CC and NA) were compared, as this period is not covered in the records retrieved from the other basins. The pollen assemblages for the three sites are similar (Fig. 7.3), with percentage *Pinus* pollen *c.* 65%, percentage *Betula* pollen *c.* 15%, percentage *Calluna* pollen *c.*15%, and both Cyperaceae/Poaceae and herb pollen at *c.* 1%. This suggests that all three sites were largely reflecting the surrounding vegetation at a

regional scale, probably as a result of being large openings with few trees. No *Pinus* stomata were observed at any of the sites.

Further south at Carn a'Chnuic, the proportion of *Calluna* pollen is highest (*c.*20%) and that of *Pinus* pollen lowest (60%). This may be the result of an increased local component for *Calluna* in the pollen signal, which is supported by the pattern of increase in percentage *Calluna* pollen coinciding with increased abundance of both macroscopic and microscopic charcoal. In chapter 5 it was suggested that human firing of this area may have begun as early as 7500 cal. BP (6500 BP), which supports O'Sullivan's (1974) interpretation of pollen assemblages from nearby Loch a'Chnuic, where he suggested that heathland formation was taking place by 6600 cal. BP (5800 BP). The regional signals from all sites indicate that *Pinus* and *Betula* were the main woodland taxa. Percentage *Alnus* pollen does not vary greatly between sites, but is slightly lower at Carn a'Chnuic. Being at a higher altitude, there may well have been less *Alnus* present here because of less favourable climatic conditions. The low levels observed at all sites probably represent its colonisation of wetter areas or watercourses in the wider landscape, *e.g.* the Spey floodplain, rather than any local presence in the basins cored.

ii) Time slice 2: 4260 cal. BP

By this time, major landscape changes are believed to have been well underway in parts of Scotland (Edwards and Whittington, 1997). Dubois and Ferguson (1985) identified the occurrence of a wet episode in the Cairngorms between 4650 cal. BP (4250 BP) and 4350 cal. BP (3870 BP) and the 'pine decline' and blanket bog inception had begun, asynchronously, in other parts of Scotland. Although these factors may have been in part linked to a decline in woodland from around 4600 cal. BP (4000 BP), Edwards and Whittington (1997) argue that the density of archaeological finds suggests that expansion of settlement and agriculture were of major importance in reducing woodland cover at this time.

From a profile from Loch Pityoulish (situated *c.* 7 km south west of Loch Garten within the Spey floodplain), O'Sullivan (1976) infers a change in forest composition from *Pinus*-dominated to *Betula*-dominated at *c.* 4300 cal. BP (3800 BP), with *Quercus*, *Alnus* and Coryloid pollen representing important subsidiary tree taxa. The dominance of *Betula* pollen over *Pinus* pollen observed is thought to have been uncommon in the Eastern Highlands so is interpreted as representing mainly local vegetation.

For Abernethy nature reserve, only two sequences for the period from 6400 cal. BP (5500 BP) have previously been published: Loch Garten and Loch a'Chnuic (O'Sullivan, 1974). O'Sullivan (1974) suggests that clearances around Loch Garten had begun by 3900 cal. BP (3600 BP), whilst further south, at Loch a'Chnuic, he infers that heathland formation was already underway, having begun by 6600 cal. BP (5800 BP). Little subsequent change in the proportions of pollen taxa occurs until peat growth commenced at the coring site itself. The stratigraphic position of this change is consistent with a date of around 4600 cal. BP (4000 BP), suggesting that peat growth began during a similar period to the climatic changes referred to above. The rapid increases in *Calluna* pollen seen from this point may reflect either an increased local component in the pollen signal from bog surface vegetation, or a rapid expansion of heathland in the surrounding area.

Comparison of pollen assemblages between sites

For 4260 cal. BP, pollen assemblages for major taxa from five sites were compared (Fig. 7.3). The similarity of the signal at site LC to that of the large bog at site NA suggests that these two sites were still reflecting regional vegetation at this time, implying that North Abernethy had not changed greatly in forest cover, but that the area east of Loch a'Chnuic had to some extent been cleared of forest by 4260 cal. BP. This is consistent with the idea of heathland development having started here much earlier, as O'Sullivan (1974) proposes. However, at Faesheallach Burn, one kilometre to the south west and *c.* 70 m higher in altitude, there is a much lower proportion of *Pinus* pollen (*c.* 30%). This suggests that this area, if not remote from trees, was much further from forested areas than Loch a'Chnuic or had a much lower density of trees. This would be consistent with *Pinus* having retreated from higher altitude areas first, whether as a result of climatic or human factors. There is strong support for tree loss being linked to climatic factors in the form of an extensive layer of pine stumps at the base of this sequence, some 80 cm below the Hekla-4 isochrone. The proportion of *Pinus* pollen at the Loch an Spioraid site is similar to that east of Loch a'Chnuic, at around 50%, although at Loch an Spioraid there is a higher proportion of *Calluna* pollen and a lower proportion of *Betula* pollen.

The percentage of *Betula* is highest at Forest Lodge; this site appears to have been recording a local signal from a wet basin that supported alder carr, and *Betula* may also have been locally present as wet birch woodland (see chapter 6). Arboreal pollen (AP) exceeds 90% and it is likely that *Alnus* was present in the basin itself, indicated by pollen proportions of *c.*20% TLP (see Huntley and Birks, 1983). At all the other sites, the proportions of *Alnus*

pollen has changed little since *c.* 6400 cal. BP (5500 BP), suggesting that its range did not change greatly following initial colonisation of its eventual niche (Birks, 1970; O'Sullivan, 1977). The proportion of *Corylus*-type pollen is lower at the Forest Lodge site, which may be a result of a reduction in flowering related to closed canopy woodland or possibly to coppicing. The consistent presence of both *Betula* and *Corylus*-type pollen across all sites may have occurred as areas of *Betula/Corylus*, woodland, possibly co-existing with pine forest.

At Carn a'Chnuic, AP levels of around 85% strongly suggest this bog had tree cover by 4260 cal. BP, supported by the presence of wood detritus in the peat. The presence of Poaceae, *Rumex* and *Plantago* pollen suggest that the tree cover was scattered, but it is likely that the arboreal pollen signal is largely a local one and that the level of *Betula* pollen recorded (10%) reflects local growth.

Changes since 6400 cal. BP

The major changes are a marked reduction in percentage *Pinus* pollen across all parts of the reserve sampled, with increases in *Calluna* pollen to levels suggestive of the beginnings of heathland development in some areas. The development of heathland seems to have been most pronounced to the south and east of the study area, *i.e.* in higher altitude, more exposed areas. This suggests that climatic factors may have operated in conjunction with human activity to bring about the loss of the forest in these areas. As the proportion of *Betula* pollen tends to increase slightly since 6400 cal. BP, this could indicate that human-induced clearance or climatic factors mainly affected *Pinus*-dominated parts of the forest. Alternatively, as *Betula* spp. are typical pioneers in cleared areas, their populations may have been able to recover more easily than *Pinus*. It may be that *Betula* existed to some extent as more distinct stands in *e.g.* wetter areas less favourable for *Pinus*. Such stands would have been relatively unaffected if *Calluna* heath developed on drier areas after clearance or climate-related loss of *Pinus* forest.

iii) Time slice 3: 2150 cal. BP

By this time, further heathland development and opening of the forest canopy are suggested by an increase in percentage *Calluna* pollen in existing pollen records for the areas. There are relatively few pollen records incorporating vegetation changes occurring around 2000 years ago for the Cairngorms area. At Loch Pityoulish, O'Sullivan (1976) suggests that local human influences such grazing were associated with canopy opening and development of

heathland from around 3200 cal. BP (3000 BP), with the first traces of cereal pollen dated tentatively by interpolation to around 1850 cal. BP (1850 BP). He suggests arable cultivation may have been taking place in the more fertile Spey Valley, rather than around the loch, at this time.

O'Sullivan's (1974) core from Loch a'Chnuic is a full sequence dating from *c.* 14,000 cal. BP (12,000 BP), although there are no age estimates for this profile. On the basis of percentage *Pinus* pollen he proposes that the area around Loch a'Chnuic was forested until last few hundred years.

Comparison of pollen assemblages between sites

Although only two profiles from this study could be used for this time slice, both show pronounced changes from the previous time slice (Fig 7.3). Both sites show quite a similar pollen assemblage, which may be a result of open conditions having developed at both sites such that they record a more regional signal. This idea is supported by the high proportion of *Calluna* pollen and a small increase in Poaceae at both sites.

Changes since 4260 cal. BP

A change since the previous marker horizon is particularly notable for the Forest Lodge profile, where the pollen record suggests a decline in *Betula* and the loss of local presence of *Alnus*. This probably reflects successional change from alder carr to bog within the basin (see chapter 6), but it could also suggest a major loss of forest cover in this area during the period following 4260 cal. BP. With the opening of the canopy around this basin, pollen source area would have increased as a higher proportion of pollen would be derived from regional, rather than local, vegetation.

At both sites, the ratio of *Pinus* to *Betula* is little changed, suggesting that what remained of the surrounding forest (reflected now at a regional scale) appears to have been of similar composition as previously, *i.e.* a mix of *Pinus* and *Betula*. There is also a significant reduction in the proportion of *Corylus*-type and *Alnus* pollen at both sites. At site LC, the much increased proportion of *Calluna* pollen and decrease in both *Pinus* and *Betula* pollen proportions suggest that substantial opening of the landscape had occurred in this area by 2150 cal. BP. The reduction in percentage *Pinus* pollen is more marked here to the east of the loch than for O'Sullivan's (1974) site to the west of Loch a'Chnuic. It may be that woodland survived in the more sheltered areas west of the loch for longer, or there may have

been more *Calluna* growing locally to the east of the Loch on higher, possibly drier ground outside the loch basin catchment, which increased the local component of the pollen signal. As discussed in chapter 5, cycles of forest opening and closure appear to have taken place several times since 4260 cal. BP, probably linked to human firing of the landscape suggested by the marked change in the charcoal signal to sustained large peaks.

iv) Time slice 4: Present day

Within the study area today, the forest is dominated by *Pinus*. A decline in *Betula* is possibly linked to the onset of commercial forestry over the past three hundred years, since *Betula* is regarded as a nuisance species by foresters (Summers, 2005). The present day distribution of *Betula* is confined to a small number of stands near Rynettin and Tulloch, and as a component of mixed stands at Garten Wood and Bognacruie (Summers, 2005). Forest cover is mainly confined to lower altitude parts of the reserve (< 400 m), with forest existing as a fragmented mosaic with bog and heath. The degree of forest fragmentation increases on the higher ground to the south and east.

Present day pine communities in the Central Highlands are found between 170 m and 640 m (Ratcliffe, 1977), but the only apparently natural altitudinal tree line still in existence in the Cairngorms is at Creag Fhiaclach in Rothiemurchus, where it reaches *c.*640 m on an extremely wind-exposed north west spur of the Cairngorms (Steven and Carlisle, 1959; Ratcliffe, 1977; Grace and Norton, 1990; Huntley *et al.*, 1997). The upper limit of *Pinus* in the Cairngorms today appears to be artificially suppressed relative to temperature because of wind speeds, but also from the effects of grazing and rocky topography (Pears, 1967; Peterken, 1996). At Abernethy Forest, the present day potential altitudinal tree line is estimated at 650 m, although only about a third of this area within the reserve supports forest at present (Taylor, 2000; Summers, 1999).

Comparison of pollen assemblages between sites

Fig.7.3 shows samples from the top 10 cm of each of the profiles to give pollen assemblages derived from very recent or present day vegetation. The most northerly sites in the study area (TH and FL) have *Pinus* pollen proportions of *c.* 80%, which is greater than in previous time slices and is consistent with their location within the most heavily forested part of the reserve today. For the two most southerly sites, LC and FB, *Calluna* pollen percentages reach *c.* 75%. At these sites, *Pinus* pollen percentages of *c.* 20% and *c.* 10% are associated with an

open landscape 1 km and 2 km respectively from the nearest *Pinus* canopy. Pollen from taxa other than *Pinus* and *Calluna* are very poorly represented, rarely exceeding 2%. *Betula* pollen is found in all sites at levels < 2%, but at one site, LS, it occurs at a proportion of *c.* 10%. This probably relates to its location near a relatively open area outside the reserve boundary where several stands of *Betula* woodland occur approximately 1 km to the north east.

Changes since 2150 cal. BP

The most obvious changes over the past 2000 years or so are the greatly increased proportions of *Calluna* pollen for sites to the south and east of the study area (LS, LC and FB), the increase in percentage *Pinus* pollen for sites in the north of the study area (TH, NA and FL), and the decrease in *Betula* pollen relative to *Pinus* pollen apparent in all assemblages. Whilst overall amount of forest cover in the northern part of the study area may be similar to that of the past, *Betula* pollen forms a minimal component of the present day signal, suggesting a loss of canopy diversity has occurred. Pollen records suggest that the decline in *Betula* is a relatively recent phenomenon (O'Sullivan, 1977; Summers, 1999; chapter 5; chapter 6). Its virtual disappearance from the regional signals from the open sites NA, LC and FB also indicates that its presence within the wider landscape is much reduced. The proportions of *Corylus*-type and *Alnus* pollen are also much reduced or absent from all sites and the pollen records suggest this too is a recent occurrence. This suggests these tree species are much rarer in the landscape than formerly. These taxa may, like *Betula*, have been removed by commercial foresters from land suitable for plantations, leaving only relict stands in less suitable areas.

Hypotheses

From comparison of the time slice pollen assemblages, two major themes were selected for further investigation. Firstly, there is some evidence to suggest a decrease in the altitudinal limits of *Pinus* between 6400 cal. BP and 4260 cal. BP, but the scale of this decrease is unknown. Also, the extent to which this alone could have accounted for the decline in *Pinus* pollen seen during this period is unclear, particularly as this coincides with the period when human activity was first detected in the pollen record.

Secondly, there are clear ideas about how, when and where humans first settled and began to impact significantly upon the vegetation at Abernethy Forest in the literature, so it would be useful to design scenarios to explore whether or not the pollen signal is consistent with

these ideas. It was decided to focus on testing the types of patterns that may have resulted from changes in the altitudinal limits of *Pinus*, changes in forest composition and changes in the amount and distribution of clearances and heathland. The following hypotheses were devised to form the basis for landscape generation:

i) the altitude of the *Pinus* tree line at 4260 cal. BP had decreased from that of 6400 cal. BP
ii) forest cover decreased throughout the landscape between 6400 cal. BP and 4260 cal. BP
iii) there was a change in forest species composition between 6400 cal. BP and 4260 cal. BP
iv) heathland was scarce before 4260 cal. BP but widespread by 2150 cal. BP
v) heathland development was more likely at higher altitudes
vi) there was no change in forest composition between 4260 cal. BP and 2150 cal. BP.

Statement i) assumes that the predominant process affecting vegetation was climatic deterioration, with conditions less favourable for *Pinus* at higher altitudes at 4260 BP. Statements ii) and iii) assume that clearance by humans had begun to impact on forest cover and species composition by 4260 cal. BP, with selective clearance of *Pinus* for fuel or building followed by an increase in *Calluna* or *Betula* in the resulting open areas. Hypotheses iv), v) and vi) are based on the assumptions that significant areas of the forest had been cleared for grazing and had become heathland by 2150 cal. BP compared to 4260 cal. BP, but the remaining forest was at this time largely unchanged in character. Changes in fire regime inferred from the records in cores LS, LC and FB in particular (see chapter 6) suggest that heathland formation was well underway and that human use of fire may have been taking place.

Methods

Empirical pollen data

For all cores, fossil pollen assemblages from depths corresponding to each time slice were used for comparison with simulated assemblages. Fossil assemblages were recalculated to give percentages of the six taxa used in the simulations. Cyperaceae/Poaceae, and *Betula*/*Corylus*-type were treated as single taxa so that all pollen taxa matched those used in

the simulations (treatment of Poaceae and Cyperaceae follows that of chapter 4; see below for treatment of *Betula* and *Corylus*).

Landscape scenario creation

The first stage in landscape scenario creation involved identifying the main plant taxa likely to be present in each time slice from the pollen diagrams. Assumptions also had to be made about the main communities present and their composition (Tables 7.1 and 7.2). As it is not possible to assess the performance of the Prentice (1985) model for *Corylus* due to its virtual absence in the present day vegetation (see chapter 4), *Betula* woodland and mixed *Betula/Corylus* woodland were modelled as both a single community and single pollen taxon on the basis of their similar pollen fall speed properties (Gregory, 1973; Broström, 2002) and ecological association (*e.g.* Tipping, 2003; *cf.* Nielsen, 2003). Bog communities were represented mainly by Cyperaceae/Poaceae and *Calluna*. The proportion of *Calluna* was estimated at 30%, slightly lower than the 35% used to simulate present day bog vegetation in chapter 4. It is difficult to assess whether or not present day bog communities are suitable analogues for past bog communities, but on balance it was decided to lower the percentage of *Calluna* for the past communities on the basis that it appears only to have greatly increased in the pollen record since 2150 cal. BP.

An Ordnance Survey DEM with a pixel resolution of ten metres was obtained for the 15 km x 15 km study area. Ordnance Survey Landline data was used to create a data layer containing information on water features such as lochs, rivers and streams, removing artificial features such as drains. In LANDSCAPE (Middleton, unpublished), ecological restraining rules (Table 7.3) were applied. For each time slice, a preliminary set of landscapes was generated using a broad range of rules to give a general indication of the types of landscapes that produce pollen assemblages similar to the fossil assemblages (*cf.* Caseldine and Fyfe, 2006).

For 6400 cal BP, it was inferred in chapters 5 and 6 that sites TH, NA and CC would have been large openings, so bogs of 100 m radius were placed in the landscape in order that the simulated assemblages would reflect the surrounding vegetation in a similar way to the fossil pollen data.

Table 7.1. Land cover types used in HUMPOL for reconstruction of past landscapes at Abernethy nature reserve.

HUMPOL code	Land cover type
0	Bare rock
1	Water
2	Open bog
3	Bog with trees
4	Swamp
5	Alder carr
6	Heath
7	Rough pasture
8	*Alnus* woodland
9	Mixed woodland
10	*Betula* and *Betula/Corylus* woodland
11	*Pinus* woodland

Table 7.2. Community compositions for land cover types selected for simulation within the landscape scenarios.

Community	*Pinus*	*Betula/Corylus*	*Alnus*	*Calluna*	Cyperaceae /Poaceae	Herbs
Rock	0	0	0	0	0	0
Water	0	0	0	0	0	0
Bog	0	0	0	30	65	5
Bog with trees	5	5	0	30	55	5
Fen	0	0	0	0	98	2
Heath	0	0	0	80	20	0
Rough pasture	0	0	0	0	95	5
Alder woodland	0	0	100	0	0	0
Alder carr	0	0	70	0	30	0
Mixed woodland	40	60	0	0	0	0
Birch/hazel woodland	0	100	0	0	0	0
Pine forest	100	0	0	0	0	0

Table 7.3. Ecological restraining rules and land cover types used to populate the landscape digital elevation model representing the period before significant human impact (*c.* 6400 cal. BP).

Rule	Resultant land cover type
0- 20 m altitude and slope 0-15°	Fen
20 – 100 m altitude and slope 0- 15°	Bog
0-400 m altitude and slope >15°, variable random patches	Birch/hazel woodland
0-400 m altitude and slope >15°, variable random patches	Birch woodland
101 -880 m altitude	Pine forest
50 m zone < 400 m altitude around lochs and rivers	Alder woodland
881 - 1100 m altitude	Heath
Slope > 65° or altitude over 1100 m	Bare rock

The landscapes which produced simulated pollen assemblages within a similar range to those of the fossil assemblages were then selected for further refinement by modifying constraining rules for each time slice and changing rules relating to the number, size and vegetation composition of randomly placed patches. By varying the landscapes in this way, it is possible to use the models to explore how altering the vegetation structure and distribution affects pollen deposition at the core sites. This in itself can offer important insights into the past character and structure of the plant communities present that can significantly improve on that available from intuition alone (Caseldine and Fyfe, 2006).

Time slice 1: c. 6400 cal. BP

Between 100 m and 880 m altitude, the landscape was classed as pine forest based on tree line estimates (Huntley *et al.*, 1997) and the idea that the forest would probably have been at its maximum extent at this time (Birks, 1988; Bennett, 1984, 1995, 1996; Tipping, 1994). A rule was included to classify any land above 880 m as open heath, but no parts of the landscape were above this altitude so forest cover was continuous above 100 m. Land below 100 m was classed as fen.

A rule was designed to place *Alnus* around lakes and alongside rivers with a probability of 0.5 to mimic scattered trees in its preferred riparian habitat (Bennett and Birks, 1990). This zone was arbitrarily extended to 50 m from the waters edge, and confined to altitudes below 400 m on the basis that *Alnus* is intolerant of cold conditions (Grime *et al.*, 1988).

Betula/Corylus woodland was restricted to altitudes below 400 m on basis of the ecological limits of modern mature (flowering) trees (Grime *et al.*, 1988). *Betula/Corylus* and *Pinus/Betula* patches were introduced to produce a mosaic of heterogeneous forest composition. It is reasonable to assume that such mosaics existed *c.* 5700 cal. BP (5000 BP; Tipping, 1994) and such distribution patterns exist in the Abernethy Forest reserve today, albeit to a limited extent. However, little is known about the relative proportions of *Pinus*, *Betula* and *Corylus* that were in the forest around 5700 cal. BP, so scenarios with a range of forest compositions were generated by changing the number of *Pinus/Betula* and *Betula* patches (25, 50 or 100 patches) and also the size of patch (500 m or 1 km diameter). A total of twenty landscape scenarios were tested.

Time slice 2: c. 4260 cal. BP

For this time slice, scenarios generated in LANDSCAPE (Bunting and Middleton, in prep.) were designed to test hypotheses i) to iii) above, *i.e.* the effects on the simulated pollen signal of changing the altitude of the tree line, size of clearance patches around the loch and within the forest and size of patches in the forest mosaic. For the tree line, three variants were used: *Pinus* to 600 m, *Pinus* to 650 m and a transitional model with closed *Pinus* to 650 m and heath with scattered trees to 750 m. The altitudinal limits of *Pinus* may have changed and fragmented quite easily because *Pinus* is particularly sensitive to climate change (Tipping, 2003). To represent clearance around lochs, two variants were used: clearance to 50 m and clearance to 100 m from the loch shore, where *Pinus* was replaced by a heath community with scattered trees. Alternatively, to represent clearance throughout the forest, the effect of random patches of heath with scattered trees within the forest was observed, seeding 5, 10, 30 and 50 patches of both 100 m and 200 m diameter. Finally, the effects of large (600 m diameter) and small (300 m diameter) patches of *Betula* and *Pinus/Betula* forest in the mosaic were investigated. 28 possible landscape scenarios were tested.

Time slice 3: c. 2150 cal. BP

For this time slice, rules were created to mimic possible processes of heathland formation, altering the proportion of heath and its distribution to explore the effect of this on the simulated pollen signal. These rules were applied to a forest mosaic created using the same rules as for 4260 cal. BP so that its composition would be similar, then the rules were varied to explore the effect of a less diverse forest on the pollen signal. The *Pinus* tree line was set at 650 m for all scenarios.

A rule was implemented to mimic the encroachment of heathland onto forested areas, which was varied so that a change from forest to heathland was constrained by altitude, firstly to altitudes above 400 m and then to altitudes above 300 m. This was based on the assumption that the effects of climatic and human factors may have operated differently with altitude. The practice of transhumance may have led to heavy grazing pressure on higher ground that was too exposed for cultivation (see Pears, 1967), which may have meant that tree regeneration was more inhibited here (*e.g.* after fire) than on lower ground. Local presence of *Alnus* at FL was modelled by placing alder carr community (Table 7.2) around the coring site to a radius of 70 m in keeping with the size of the basin today. Patches of heathland were placed randomly into the landscape, varying the amount of cover by both changing the size

of patches (1 km and 2 km diameter patches) and the number of patches seeded in the landscape (50, 100 and 150 patches). A total of 44 possible landscape scenarios were tested.

Simulation of pollen assemblages

Pollen assemblages for the coring site locations were simulated for each landscape scenario using PolFlow (Middleton and Bunting, 2005). Pollen productivity estimates (PPEs) from southern Sweden were used for all taxa (see Table 4.2) as these were shown to work well for major pollen taxa (chapter 4). Several of the early model runs were also performed with the UK *Alnus* PPE (Bunting *et al.*, 2005), but this was found to produce simulated pollen percentages for *Alnus* which were several orders of magnitude greater than those observed in the fossil record. The Swedish estimate was therefore selected for subsequent model runs. The community compositions used for all simulations are shown in Table 7.2.

Selection of best fit scenarios

In order to identify which, if any, of the simulated pollen assemblages were the closest matches to the fossil pollen samples, dissimilarity coefficients were used. These measure the differences between multivariate samples (Overpeck *et al.*, 1985) and are commonly used in the modern analogue technique to identify modern analogues for fossil assemblages (*e.g.* Janssen, 1966; Overpeck *et al.*, 1985; Williams *et al.*, 2001; Gavin *et al.*, 2003). The program ANALOG (Schweizter, 1994) was used to calculate the squared chord distance dissimilarity measure for each simulated assemblage, using Overpeck *et al.*'s (1985) cut-off value of 0.15 to determine which of the simulated assemblages were a statistically valid match for each fossil assemblage. The dissimilarity coefficients for all simulated assemblages were then compared for each time slice to identify which landscape scenarios produced the best fit overall. As this is a new approach, no standard method for selection of best fit across multiple sites yet exists, so both mean rank mean dissimilarity coefficient and lowest overall mean squared chord distance were calculated for each scenario to identify the most feasible landscapes.

Results

Calculation of mean rank mean dissimilarity coefficient produced the same best fit landscape in all but one case, as the differences in coefficient values were small. Where there are large variations in the values of dissimilarity coefficients between sites, mean rank may be a more

suitable method as a particularly large or small mean value for one site would skew the result. Dissimilarity coefficients for landscapes, with the lowest mean squared chord distance are shown in Table 7.4. In Table 7.5, the percentage composition of the communities for the best fit landscapes and present day vegetation cover classified using the same categories are shown. In the text these values are rounded to the nearest 5%.

For 6400 BP, seven of the 20 landscapes tested satisfied the dissimilarity coefficient cut-off value of 0.15 for all sites (Appendix 3). Characteristics common to all feasible landscapes were *Alnus* growing to 400 m (*c.* 10% cover) and forest cover dominated by pine forest (*c.* 80%) with mixed *Pinus/Betula/Corylus* woodland at *c.*10% cover and birch woodland at *c.* 1% cover (Table 7.5). In the most feasible landscapes, pine forest extended to a tree line of 880 m, but a tree line of 700 m also produced a feasible landscape. The area of heath and bog was less than 1%. The least similar landscapes were those where birch and mixed woodland were dominant below 400 m.

For 4260 cal. BP, 16 of the 27 landscapes satisfied the dissimilarity cut-off criteria (Appendix 3). The most feasible landscapes were those with *c.* 60% pine forest cover, *c.* 5% heath cover, *c.* 15% mixed woodland and *c.* 15% birch woodland, a significant increase from values for the feasible landscapes of 6400 cal. BP; Table 7.5). Unfeasible landscapes were those with the largest number of random clearance patches or fewer/smaller patches of birch and mixed forest.

For 2150 cal. BP, 38 of the 44 sites satisfied the dissimilarity cut-off criteria (Appendix 3). The most feasible landscapes had a *c.* 30% pine forest cover with a further *c.* 15% mixed forest and *c.*10% birch woodland. Heathland was dominant above 400 m altitude, with a total cover of *c.* 60%, a large increase since 4260 cal. BP (Table 7.5). Unfeasible landscapes had similar amounts of heathland > 400 m altitude but less birch or mixed forest in the remaining woodland.

The 'best fit' landscape scenarios are shown as a series of 'palaeo-maps' alongside the present day landscape in Fig. 7.4. These show a progressive decrease in forest cover, with greater proportions of *Betula/Corylus* and mixed forest at 4260 cal. BP than at other times, and a pattern of heathland development that is largely restricted to areas of higher ground over 400 m altitude. The reconstruction suggests that at some time between 2150 cal. BP and the present day, the forest changed from being quite mixed to almost exclusively *Pinus* forest

and the area of remaining forest may have decreased by half during this time from *c.* 30% to 15% (Table 7.5). By far the most dominant vegetation type at present is heath or bog at *c.* 85%.

Table 7.4. Summary of squared chord distance dissimilarity coefficients for each profile for the 'best fit' landscape scenario for each time slice. The presence of a dash indicates that a profile was not used in the reconstruction of the time slice. All dissimilarity coefficients fall below the 0.15 cut off level of Overpeck *et al.* (1985).

Site	TH	FL	LS	NA	CC	LC	FB	mean *(s.d)*
Time slice 1: 6400 cal. BP	0.089	-	-	0.027	0.036	-	-	0.051 *(0.034)*
Time slice 2: 4260 cal. BP	-	0.094	0.078	0.046	-	0.056	0.062	0.067 *(0.019)*
Time slice 3: 2150 cal. BP	-	0.057	-	-	-	0.061	-	0.059 *(0.002)*

Table 7.5. Percentage cover of communities for best fit past landscapes and the present day, expressed as a percentage of total vegetation cover and, for woodland, as a percentage of total woodland cover.

	Percentage land cover			
Vegetation community	**6400 cal. BP**	**4260 cal. BP**	**2150 cal. BP**	**0 BP**
Heath or bog	0.03	6.16	58.50	86.06
Mixed forest	11.57	15.41	4.46	0.29
Alder woodland	6.53	6.50	1.96	0.06
Birch/hazel woodland	1.48	12.98	4.66	0.14
Pine forest	80.39	58.95	30.46	13.45
Total percentage wooded	99.97	93.84	41.54	13.94
% of all wood non-pine dominated	19.59	37.18	26.67	3.52
% of all wood pine dominated	80.41	62.82	73.33	96.48
% of all wood mixed forest	11.57	16.42	10.74	2.08
% of all wood birch/hazel	1.48	13.83	11.23	1.02

Fig. 7.5 shows the observed and simulated pollen assemblages for all sites for each time slice. For the first time slice, both simulated and observed assemblages are similar across the

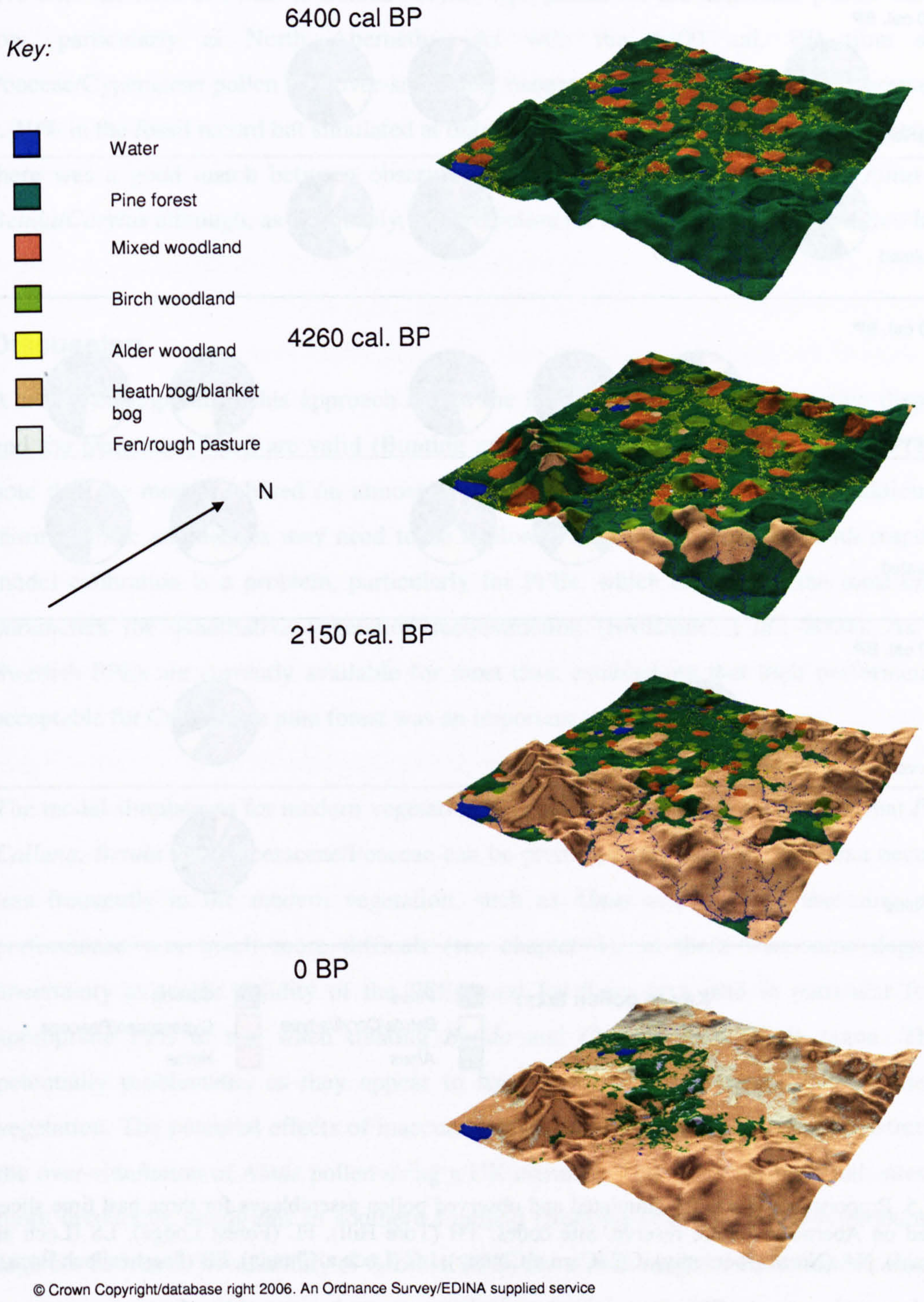


Fig. 7.4. Feasible landscape scenarios for three past time slices modelled using six vegetation communities for a 15 km x 15 km study area centred on Abernethy nature reserve. The fourth time slice shows present day vegetation mapped from a reclassification of satellite imagery. Vertical exaggeration on the digital elevation model was set at 3.0.

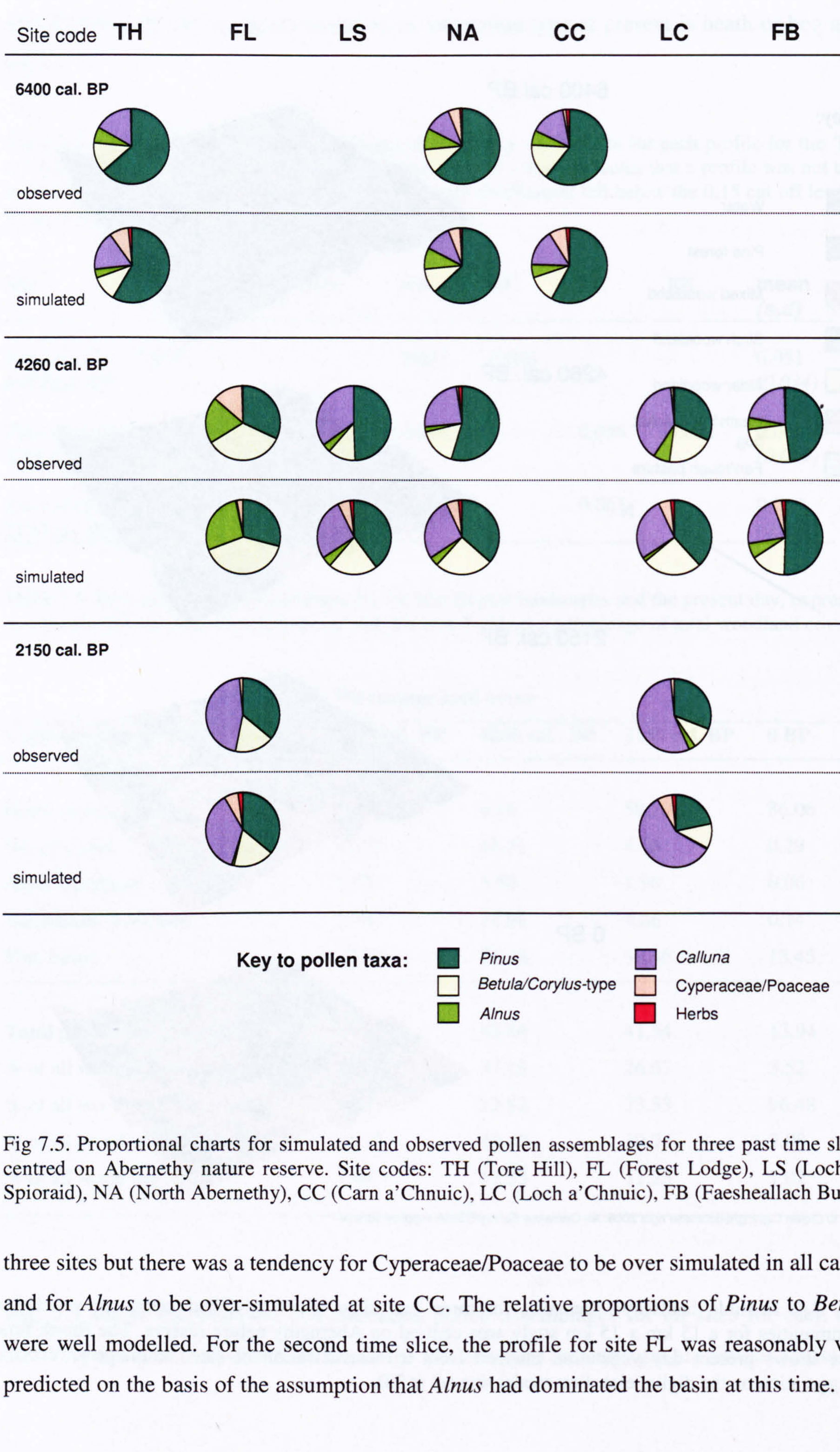


Fig 7.5. Proportional charts for simulated and observed pollen assemblages for three past time slices centred on Abernethy nature reserve. Site codes: TH (Tore Hill), FL (Forest Lodge), LS (Loch an Spioraid), NA (North Abernethy), CC (Carn a'Chnuic), LC (Loch a'Chnuic), FB (Faesheallach Burn).

three sites but there was a tendency for Cyperaceae/Poaceae to be over simulated in all cases, and for *Alnus* to be over-simulated at site CC. The relative proportions of *Pinus* to *Betula* were well modelled. For the second time slice, the profile for site FL was reasonably well predicted on the basis of the assumption that *Alnus* had dominated the basin at this time. For

the remaining sites, the best fit landscape effectively modelled the relative proportions of *Calluna* pollen between the sites. Total AP was reasonably well simulated, but in four of the five sites the ratio of *Pinus* to *Betula/Corylus*-type pollen for the simulated pollen was too low, particularly at North Abernethy. As with the 6400 cal. BP time slice, Poaceae/Cyperaceae pollen was over-simulated, except for site FL where it was observed at *c.* 10% in the fossil record but simulated at only 3% (Fig. 7.5). For the 2150 cal. BP scenario, there was a good match between observed and simulated pollen for *Calluna*, *Pinus* and *Betula/Corylus* although, as previously, the prediction for Poaceae/Cyperaceae was too high.

Discussion

A major assumption of this approach is that the Prentice-Sugita model of pollen dispersal and the parameters used are valid (Bunting *et al.*, submitted). Jackson and Lyford (1999) note that the model is based on atmospheric parameters relating to neutral conditions, so more realistic alternatives may need to be explored. However, uncertainty with respect to model calibration is a problem, particularly for PPEs, which are one of the most critical parameters for quantitative vegetation reconstruction (Broström *et al.*, 2004). As only Swedish PPEs are currently available for most taxa, establishing that their performance is acceptable for Caledonian pine forest was an important step.

The model simulations for modern vegetation data presented in chapter 4 suggest that *Pinus*, *Calluna*, *Betula* and Cyperaceae/Poaceae can be predicted satisfactorily. For taxa occurring less frequently in the modern vegetation, such as *Alnus* and *Corylus*, assessing model performance was much more difficult (see chapter 4), so there was some degree of uncertainty as to the validity of the PPEs used for these taxa, and in particular for the appropriate PPE to use when treating *Betula* and *Corylus* as a single taxon. This is potentially problematic, as they appear to have been important components of the past vegetation. The potential effects of inaccurate PPEs within the model were demonstrated by the over-simulation of *Alnus* pollen using a UK estimate. This was obtained from sites with more favourable conditions in southern England (Bunting *et al.*, 2005) so is probably too high for Scotland. Availability of Scottish PPEs for a wide range of communities would go some way towards addressing these uncertainties. As yet, it is difficult to understand PPEs and therefore set the input parameters for the model.

The landscape scenarios generated were purposefully simple, to explore the effects of specific landscape changes on the simulated pollen assemblages. Knowledge of plant autecology provided a useful basis for landscape design, but in reality many of the factors affecting woodland development are multi-faceted and therefore difficult to model (Birks, 1989). Factors such as climate may involve changes in precipitation, seasonality and temperature, all of which exert variable influences on different woodland taxa and overall woodland development over space and time. In the context of mid-Holocene woodland development, the establishment and spread of some taxa into new areas in the landscape will also have involved an element of chance (Edwards and Whittington, 1997).

Other abiotic features of the landscape that may have varied during this time include sea levels, the height of the water table and the sizes of water bodies. Whilst modelling sea level changes could be regarded as crucial only for coastal sites, other hydrological changes would have been important at some stages in the development of all pollen-yielding sedimentary basins. Such changes could have occurred in response to regional factors such as climate change or local factors such as hydrological changes or basin infilling processes. From the palaeoecological studies, it was possible to use site stratigraphy with the pollen record to infer both regional and local changes in hydrology in some instances (see chapters 5 and 6). For the reconstruction, this allowed appropriate vegetation communities to be modelled within the basins for each time slice, *e.g.* open bog at sites NA, TH and CC in the first time slice and alder carr at site FL in the second time slice.

Assumptions also had to be made about community composition for input into the model. To some extent, the composition of modern communities can be used as a basis for these assumptions, but for some communities the availability of modern analogues is limited. There is no modern analogue for the past distribution and abundance of *Corylus*, which in the early Holocene remained more abundant relative to other taxa than is seen today, possibly as a result of a unique combination of climate and fire conditions (Huntley, 1993). Similarly, there are few analogues for the *Betula/Corylus* woodlands of the early Holocene, one reason being that competition from other tree taxa would have differed from that of today (Tipping, 2003). Combining *Betula* and *Corylus*-type pollen for modelling purposes meant that it was not possible to make any deductions about the former extent of *Corylus* at Abernethy Forest, but also minimised the possibility of making false inferences. The consistent over-simulation of Cyperaceae/Poaceae suggests that the PPE used was too high or that its presence in the vegetation communities was over-estimated. Alternatively,

differences in height may affect pollen dispersal. Cyperaceae species are generally taller than Poaceae, but as yet differential pollen release height is not incorporated into the Prentice-Sugita model.

Over long timescales opening size changes have implications for reconstruction, but from the hypothetical landscapes tested in chapter 4, it does not appear that the relevant source area of pollen would have varied significantly for openings between 30 m and 100 m radius, so changes through time probably did not significantly change the area of the surrounding vegetation being represented in the pollen record. Where there was direct evidence for local tree presence that could indicate a decrease in opening size or basin composition, this was incorporated into the rules by changing the community occupying the basin, *i.e.* placement of alder carr at site FL, which resulted in a more local signal being obtained. Random placement of heathland will also have caused canopy opening around the sampling point, as occurred for sites LS, LC and FB in the 2150 cal. BP time slice. The vegetation composition assigned to each basin remained unchanged, with same bog community used for each time slice. In reality, there was likely to have been a change in the composition of the bog community in response to processes such as basin succession and human activity, which may have affected the influence of local plants such as *Calluna* on the pollen signal.

Only a limited set of scenarios were tested here to investigate the effect of selected parameters. There will be many more feasible scenarios that vary in aspects not thoroughly investigated, such as the size, shape and frequency of patches of all vegetation communities (see Bunting *et al.*, accepted) and equifinality might be expected, *i.e.* multiple landscapes with different mosaics will have simulated pollen assemblages that are equidistant from the fossil assemblage (Bunting et. al, accepted). The simulated pollen assemblages act as a tool for assessing the validity of past landscapes, where previously there was no objective method of evaluating hypothetical landscapes.

As this is a novel way of applying the MSA, there is as yet no standard method for selection of the best fit landscape across several sites. Of the two methods tested, calculation of mean rank mean dissimilarity coefficient produced the same best fit landscape in all but one case. Mean rank may be a more suitable method if there are large variations in the values of dissimilarity coefficients between sites, as a particularly large or small value for one site may skew the result if the mean is used.

When using tephra isochrones for reconstruction, an important issue to consider is the possibility of significant direct or indirect effects of the tephra fall itself, which may produce an isochrone with a pollen signal that does not reflect the typical vegetation pattern of the century. Apparently temporary changes in pollen assemblages (*i.e.* decreases in pollen proportions for the previously dominant tree taxon) were noted for core s NA and FL, but for the other cores finer resolution pollen analysis around the peak concentrations of tephra may have detected other such anomalies. Also, if the effects of tephra deposition are in any way localised, this could give rise to more distorted 'snapshots' of long-term forest development, which may lead to reconstructions based on short-lived states that are not typical in the context of long-term change .

c. 6400 cal. BP reconstruction

For this reconstruction, the application of simple ecological rules produced scenarios that matched the fossil pollen assemblages well, suggesting that ecological preferences of tree taxa around this time were major determinants of forest distribution within the study area. The three regional cores could not be used to detect changes in the proportion of *Pinus* pollen in relation to the height of the tree line *per se* as smaller scale studies would be required for this (*e.g.* McConnell, 1996). Alternatively, cores could be taken at the most sensitive locations, using the model to identify where such changes are most likely to have occurred.

The simulations were useful in indicating that the predominance of percentage *Pinus* pollen in the assemblages could in most cases only be replicated for a landscape with around 80% forest cover. This supports existing ideas (Birks, 1988; Bennett, 1984, 1995, 1996; Tipping, 1994; Huntley *et al.*, 1997; MacKenzie, 2002) that open areas were not extensive in the area at this time. It is likely that the altitudinal tree line was determined more by topographic features such as the presence of screes and cliffs than by climate restraints (see Peterken, 1996).

c. 4260 cal. BP reconstruction

This reconstruction suggests a landscape with a higher proportion of *Betula/Corylus* and mixed forest than existed at 6400 cal. BP. Reducing the altitude of the tree line for *Pinus* from 750 m to 600 m did not in itself produce feasible landscapes, suggesting that other factors were likely to have been operating to bring about a change in forest composition. All tree line movement would have occurred beyond the relevant source area of pollen (RSAP)

for the basins studied (see chapter 4), therefore will only have affected the background component of the pollen signal. However, the proportional contribution of background pollen to the pollen percentages would also change if the composition and position of vegetation within the RSAP changed, so it is not possible to attribute the decrease in *Pinus* pollen percentages to tree line movement.

An increase in the proportion of *Calluna* and *Betula/Corylus*-type pollen in the fossil record for all sites may have related to succession of *Betula* and *Corylus* into open areas occupied by *Pinus* before disturbances such as shifting agriculture. Modelling clearances as patches of heath with scattered trees did not produce landscapes that could predict the levels of *Betula/Corylus*-type pollen seen in the fossil samples. It may be that edge effects, which are not incorporated into the model, include an increase in pollen production for tree taxa at the edges of patches that may be sufficient to explain changes in their relative pollen proportions. Another possible explanation is that the level of early human activity related to forest clearance may have increased forest diversity at this stage, and encouraged a wider mix of tree species than had previously been present. Tipping *et al.* (1999) found similar patterns in the East Grampians and south east Scotland, and propose that increased diversity relates to woodland clearance for settlement. They suggest that the gaps created were of sufficient duration, size or character to provide niches for late-arriving or poorly competitive taxa. The findings at Abernethy are consistent with the hypothesis that there was a change in forest composition between 6400 cal. BP and 4260 cal. BP, and that this was at least in part a result of human activity.

It is also possible to detect other changes that may be related to human activity, such as the beginnings of heathland development or lowering of the *Pinus* tree line, suggested by the increase in percentage *Calluna* pollen at the higher altitude sites RB and FB. This is reflected in the pattern of heathland for best fit landscape (Fig. 7.4). This supports the hypothesis that forest cover had decreased at higher altitudes since 6400 cal. BP. If heathland were encroaching from above the tree line, this may suggest climatic sensitivity or possibly Mesolithic burning and grazing of the upper forest limits, as discussed by Tallis and Switsur (1990).

c. 2150 cal. BP reconstruction

As only two sites were used for this reconstruction, it is difficult to make specific inferences about the pattern of landscape change for this time slice. However, the similarity of both

fossil assemblages suggests that the areas around FL and LC were open with assemblages dominated by regional pollen. Accordingly, all the best fit landscapes showed extensive heathland > 400 m, supporting the hypothesis that widespread heathland development had occurred by this time. Scenarios with random patterns of heathland development did not produce feasible landscapes, suggesting that the idea of heathland development being strongly related to altitude is a plausible one. This suggests that the effects of human activity (inferred from the charcoal records for this period) were acting in conjunction with altitude-related climatic factors to bring about loss of forest from higher ground.

The best fit landscapes for this time slice showed a decrease in the amount of *Betula/Corylus* and mixed forest since 4260 cal. BP, which suggests that there had been a change in the composition of the remaining forest by 2150 cal. BP. This may relate to a changing pattern of land use by humans such as the move towards a more settled economy. As suggested above, earlier activities may have been at a level of intensity that positively encouraged increased compositional and structural diversity of the forest. However, by 2150 cal. BP, opening up of the forest appeared to be operating at such a scale and intensity that the process of change to heathland became irreversible and regeneration of broad-leaved species had decreased, possibly through selective removal or grazing pressure. It is possible that the area of forest contracted by increased fragmentation at the forest edge in higher altitude areas, as *Pinus* in these areas would have been both more exposed to climatic extremes and more accessible for burning and cutting.

Conclusions

It would be particularly useful to obtain PPEs for Scotland and to examine the 'edge effect' on pollen productivity for major tree taxa in mixed landscapes to produce more robust outputs from the Prentice-Sugita model for Caledonian pine forest. Whilst the scenarios presented here give a general indication of which hypotheses about landscape development are plausible, generation of large swarms of scenarios would reveal a fuller range of feasible landscapes and give a better idea of the full range of landscape variation possible for a particular fossil pollen signal. The 'time slices' presented here are illustrative of the potential for this type of hypothesis testing approach, but should not be taken as definitive in any way.

No attempt was made to model the effect of soils on vegetation distribution. As well-drained glacial moraine deposits between 200 m and 500 m are particularly suitable habitats for *Pinus*, the addition of soil and geological information to future analyses may allow refinement of the ecological rules relating to the distribution of tree taxa within the forest.

Theories about human interaction with the Abernethy environment have relied chiefly on inferences made from the peat profiles presented in this project, in conjunction with existing published work. This has been necessary as a result of the paucity of archaeological evidence for specific human activities in the area. Field surveys around known settlement sites could yield useful information, *e.g.* identifiable charcoal which, if found, could give information on the types of trees being exploited in different locations over time. Palaeoecological analysis of small sites from nearby areas could also yield information on the patterns of human activity at a smaller scale since, even with multiple sites, the scale of this study meant that only more general inferences could be made.

An important outcome of this work is that it provides a broad, long-term context that can be used as a basis for developing testable hypotheses relating to more specific questions, thereby allowing effective targeting of future effort. Future work could involve using the MSA with palaeoecological data of higher spatial and temporal resolution to address smaller-scale questions relating to important issues for conservation management. The MSA can be used to address specific questions focusing on the past few hundred years, such as exploring loss of broad-leaved species from the forest or the impact of fire and human activity on forest composition and extent. More sites from higher altitudes can be investigated to study possible mechanisms for changes in tree line and heathland development, subject to the availability of suitable sediment. For this period, possible landscape scenarios can be tested against fine resolution fossil pollen data and historical records to improve the robustness of the reconstructions (see Nielsen, 2004). Reconstructions at spatial and temporal scales of direct relevance to ecology will be particularly useful for informing conservation management for the future in a changing environment.

Chapter 8. Applications of palaeoecology to conservation management of semi-natural pine forests

Introduction

Nature conservation in western and central Europe usually involves the protection of rare or threatened native species or assemblages of species. Habitats may also be targeted for conservation in their own right, but in general an important aim is to maintain examples of natural and semi-natural ecosystems and habitats, which are selected to help ensure the survival of the species of conservation concern (Peterken, 1993; Birks, 1996). This chapter discusses the contribution that palaeoecological and pollen dispersal modelling techniques can make to established and new approaches to conservation decision making and practice. Using a case study approach, results obtained from palaeoecological records and modelling-based landscape reconstructions are discussed in relation to conservation implications for Caledonian pine forest.

If conservation management practices are to be effective, it is important to understand as far as possible the history of the habitats and species of conservation interest as well as the present character of the site (Green and Dolman, 1988; Sutherland and Hill, 1995; Rackham, 1998). When evaluating a site for conservation management planning, many attributes can only be properly assessed in the context of the long-term history of the site, *i.e.* at least the past few hundred years. Understanding as far as possible whether the current landscape is in a state of change or relative stability, and whether it is still responding to recent disturbances or is at a stage within a cyclic process can be regarded as crucial for future planning.

Over such timescales, processes themselves cannot be measured directly but it is possible to examine changes in species abundance and distribution, which can be assumed to result from changes in processes. It is then possible to explore system stability and resilience and hence how the system may respond in the context of management intervention. As many of these changes may not be apparent to a single generation of land managers, a long-term approach to future management is required, which involves consideration of other processes that operate over the long-term, such as global climate change.

As discussed at the beginning of chapter 2, many ecological processes operate at time scales beyond a human lifetime. Palaeoecology is often the only source of information available to assess how a landscape has arrived at its current state. Palaeoecology can give insights into

the 'naturalness' and fragility of a landscape, and can also be used to make inferences about the nature of past and current processes that take place over time periods not reliably covered by historical and management records (Birks, 1993; 1996).

The importance of long-term *vegetation dynamics*

Understandably, our perception and management of ecosystems has evolved to operate within timescales of human understanding, but this approach is not a sufficient basis for effective future planning. Many processes involving long-lived species such as trees appear to operate over very long time scales (*e.g.* thousands of years), whilst others, such as the *Calluna* life cycle, operate over shorter periods such as decades (Gimingham, 1972). Short-lived disturbances such as fire events may be vital for the long-term functioning of the system (Pyne, 1984). Anthropogenic influences may involve practices that took place on relatively short-term timescales, but the consequences for the landscape may be long-term or irreversible (*e.g.* the effect of grazing regimes on heathland development). Other influences may operate over much longer timescales, making their impacts difficult to understand. (*e.g.* climate change). It is therefore fundamentally important that the likely responses of plant and animal communities to conservation management practices are better understood, in order that goals set are realistic and achievable.

Approaches to conservation

Willis (1993) notes that present ecological research tends to focus on what can be observed in the present with little regard for the past, even though it may be erroneous to assume that present day vegetation and processes reflect those of the past. Many current landscapes are products of practices that are no longer being carried out (Legg, 1995; Birks, 1996). Where the goal of conservation is to maintain or restore the conditions associated with traditional practices, it may be necessary to devise alternative treatments to achieve a similar effect that are more appropriate for modern day economic and social conditions (Kirby,1993).

Conservation of species and habitats

The tendency within nature conservation has largely been to focus on protecting species, habitats and landscapes. There is an underlying assumption that the targets of conservation are not moving (Delcourt and Delcourt, 1998), and this approach appears to have led to a philosophy of maintaining the *status quo* of a site. In Britain, this is further reinforced by statutory nature conservation requirements. In the context of woodland conservation, Peterken (1996) argues that conservative attitudes such as this may inhibit the development

of new approaches for improving wildlife habitats under certain conditions. Conservative management may be necessary for poorly wooded, intensively cultivated landscapes where the capacity for woodland regeneration is inhibited by damaged soils and isolation from potential colonisers. However, in upland areas of northern and western Britain there are more refuges for wildlife outside of wooded areas, which should allow exploration of new approaches to management (Peterken, 1996).

Conservation of processes

An example of a recent shift in approach that may affect the way future conservation management progresses is the need to conserve and manage processes both within an ecosystem and beyond, rather than focusing solely on habitats and species (Delcourt and Delcourt, 1998; Balmford *et al.*, 1998). These processes may be intrinsic to the ecosystem itself, take the form of threats or be dynamic responses to external factors (Balmford *et al.*, 1998). This is an important development in the context of unprecedented global climate change, but presents a huge challenge, as identifying and understanding processes that have shaped a landscape (and may or may not still be operating) is more difficult than monitoring present day habitats or species populations. In particular, many ecosystems have been extensively modified by human activity over hundreds if not thousands of years, making it difficult to separate non-human impacts, such as past climate change, from human impacts on the landscape (Donnegan *et al.*, 2001).

Restoration and enhancement

Where ecosystem restoration or habitat enhancement is a management goal, it is necessary to know what it is that we are trying to restore to (Birks, 1996). This is not a straightforward process, as a baseline is needed from which to design appropriate restoration models. For semi-natural woodlands in Scotland, Tipping *et al.* (1999) note that the practice of using remaining woodland fragments as a model for defining the potential woodland composition of an area is inadequate, as such fragments may not be derived from native stands, may be in locations sheltered from grazing or may have been previously modified by management. An alternative is to base a restoration model on a concept of what the landscape was previously like, but if many changes have taken place, the question of which previous state arises: *e.g.* that of pre-industrial times, or an earlier, more 'natural' landscape? (Birks, 1996). In this context, 'natural' can be broadly defined as a process, situation or system more or less free of human influence (Anderson, 1991), but as Götmark (1992) points out, this may not always be the best option for achieving conservation goals.

The role of cultural factors should also be taken into account, as these will influence perceptions of what is considered a 'natural' landscape or a 'desirable' landscape, and such perceptions may be subject to change over much shorter timescales than the period for which most management plans are designed. Anderson (1991, 1992) stresses the importance of developing robust techniques for defining 'naturalness' as a scientific concept, but this is an ongoing debate (*e.g.* Götmark, 1992; Angermeier, 2002) and concepts such as desirability remain even more open to interpretation. If a desired state is one which in the past evolved from vegetation types that no longer exist, it may not be achievable. It may be necessary to look more closely at issues such as cyclic changes and species recovery patterns in order to design a more feasible model for restoration.

Palaeoecology and ecology

Although palaeoecology has evolved as a separate discipline from ecology and has in the past focussed on general construction of regional vegetation history and the behaviour of dominant taxa, in recent years the need for closer links between the two has been recognised (*e.g.* Tallis, 1991; Birks, 1993; Davis, 1994; May, 1994). Improvements in palaeoecological techniques (*e.g.* high resolution sampling, improved dating) now allow palaeoecological data to be used to address practical questions at temporal and spatial scales relevant for ecologists and nature conservationists (Davis, 1994; Birks, 1996). May (1994) suggests that most important problems in conservation and ecological management need to be considered at greater spatial scales and longer time periods than has traditionally been the norm. There is an important future role for palaeoecology in the development of a more process-focused approach to conservation, as it is now possible to study long-term processes at a wider range of temporal and spatial scales than previously.

If a fine resolution approach is taken, this can be time-consuming and a more intensive sampling approach limits the number of sites that can be investigated (see chapter 2). An alternative or supplementary tool is modelling, and in palaeoecology, recent conceptual advances in the field of pollen analysis have led to development of pollen dispersal and deposition models. Such models can make an important contribution to the quest for a quantitative way of reconstructing past vegetation from fossil pollen records. They can be used to simulate pollen data for hypothetical and real landscapes, which allows both exploration of how vegetation is reflected by the pollen signal and testing of hypotheses by comparison with fossil pollen data. An important application of these models is to the

reconstruction of past cultural landscapes, which is useful for investigating vegetation-climate feedbacks caused by human activities (Sugita *et al.*, 1999). Work is ongoing to empirically test these models for implementation at temporal and spatial scales relevant to areas of research such as climate change, archaeology and conservation management (*e.g.* Nielsen, 2003, 2004; Broström *et al.*, 2004; Hellman *et al.*, 2005).

There is also scope for developing pollen-based landscape reconstruction techniques into predictive tools that can be applied within ecological and conservation management to address pressing environmental concerns. Such tools have the potential to be applied to a range of situations as pollen is widely available and has been shown to give a useful record of past changes (Tipping *et al.*, 1999). Predictive tools based on palaeoclimate proxies (*e.g.* from deep sea sediment and ice cores) are already widely used from the global to the site scale in climate change research (Hannah *et al.*, 2002), and could be developed for other system processes at regional or local scales.

Aims

Based on the work of previous chapters, for Caledonian pine forest landscapes this chapter will critically assess: i) the contribution that palaeoecology and pollen-dispersal modelling techniques can make to conservation decision-making and practice ii) the potential contribution of landscape reconstructions based on pollen dispersal modelling to long-term management planning; iii) specific insights gained from this study and the implications for future management that arise from these, and iv) strengths and limitations of the approaches taken and future directions such work could take.

Although the work discussed here relates to semi-natural pine forest in Scotland, many of the points discussed will have wider relevance, *e.g.* to boreal coniferous forest landscapes of northern Eurasia and North America where moderate to severe human impact has occurred. Semi-natural pine forest in Scotland was fragmented in prehistoric times, and what remains has been heavily modified by human activity such as felling, burning, grazing, drainage modification and, from the eighteenth century onwards, planting (Steven and Carlisle, 1959; Peterken, 1996). In the twentieth century, widespread conversion to plantation and renewed logging of the remaining fragments took place despite their being among the most extensive examples of semi-natural woodland in Britain (O'Sullivan, 1973; Ratcliffe, 1977). Thus in pine forest nature reserves, many current management issues relate to ameliorating some of the effects of recent commercial forestry activities to allow a more natural state to develop

(Summers, 2005). An understanding of the status of the forest prior to commercial exploitation is therefore fundamental for identifying appropriate restoration goals.

A case study: Abernethy nature reserve, Inverness-shire

Site description

Abernethy nature reserve, Inverness-shire, is the largest remaining fragment of semi-natural pine forest in Britain (Summers, 2005) and is owned and managed by the Royal Society for the Protection of Birds. The site has numerous statutory nature conservation designations. A description of the site is given in chapter 1, where aspects of long-term vegetation dynamics that need more research are identified, *i.e.* past stand-scale dynamics, particularly in relation to forest and field layer structure and composition, the nature and spatial pattern human impact prior to the eighteenth century and, of crucial importance, changes in long-term fire regimes at regional and local scales. The implications this lack of knowledge may have for forest management were then identified. A series of studies was presented in chapters 3 to 7 with the aim of increasing understanding of long-term vegetation dynamics in Caledonian pine forest by determining for Abernethy nature reserve: i) changes in forest openness and species composition; ii) spatial and temporal patterns in the development of heathland; iii) regional and local long-term fire histories and iv) evidence for the onset and intensification of human activity. Here, the results of the above studies will be discussed in relation to the chapter aims.

Current management at Abernethy nature reserve

When restoring natural woodland, it is necessary to have a clear idea of what the form the restored woodland will take. Peterken (1996) defines three main options for restoration or re-creation of natural woodland in Britain: original natural, comprising all species present *c.*5700 cal. BP (5000 BP); present natural, comprising locally native trees and shrubs with others that may colonise naturally; and future natural (all native, naturalised and planted species that may colonise by natural regeneration in the future). Present-natural is the model used by the RSPB at Abernethy nature reserve, which equates to the state that it is assumed would prevail now if people had not become a significant factor. This approach involves interventions such as site restoration *e.g.* removal of drains, and control of species composition *e.g.* removal of planted or naturalised tree species and re-introduction of trees or shrubs that were once present. It is important to allow time for patterns and balances

reflecting natural features and processes to develop but there may also be a need to simulate disturbance (Peterken, 1996).

The overall management aim at Abernethy nature reserve is to develop a self-sustaining native pine forest over all areas below the present day altitudinal tree line where trees would have been a natural component (Taylor, 2000). Actions to achieve this include leaving existing semi-natural woodland unmanaged (except for deer), encouraging natural regeneration of *Pinus* and associated broad-leaved species, removal of exotic conifers and restoring drainage (Taylor, 2000). Recent work has included the removal of plantations from ploughed areas in the north of the reserve, thinning to encourage increased age, structural and species diversity of stands and restoration of wooded bogs under the EU Wet Woods LIFE project (Egret Consultancy, 1999; McHaffie *et al.*, 2000). Regeneration is encouraged by managing deer population densities (Beaumont *et al.*, 1995).

As identified in chapter 1, it should be possible to refine existing management or better justify the implementation of new practices to meet the above objectives on the basis of further knowledge of the long-term dynamics of the site. More information on long-term dynamics will also provide a baseline for improving restoration models.

Methods

This thesis focuses particularly on increasing understanding of fire history, changes in forest composition and heathland dynamics by analysing palaeoecological records (pollen, charcoal, peat stratigraphy and *Pinus* stomata) from two regional and five local sites from a 15 km x 15 km study area at Abernethy nature reserve (see chapter 1,Fig 1.1). Peat cores dating from *c.*8900 cal. BP (8000 BP) to the present day were interpreted with the aid of zoned pollen diagrams and compared with existing dated profiles for the region to establish approximate ages for zone boundaries (chapters 5 and 6).

The Prentice-Sugita model of pollen dispersal and deposition (Prentice, 1985; Sugita 1993, 1994) is then validated for Caledonian pine forest using empirical vegetation data derived from ground survey and satellite imagery using ESRI ArcView v. 9.0. Pollen rain was simulated for the landscape, and simulated pollen counts were obtained, which were compared with modern surface sample data to assess model performance (chapter 4).

The results from the palaeoecological studies are then used in chapter 7, where three time slices are identified for landscape reconstruction on the basis of the occurrence of a rise in *Alnus* pollen percentages dated to *c.* 6400 cal. BP (5500 BP) and volcanic ash deposits dated to 4260 cal. BP (3830 BP) and 2150 cal. BP (2100 BP). Possible landscape scenarios for each time slice were then created for testing against fossil pollen data. The landscapes are based on a digital elevation model to which ecological rules relating to the distribution of plants are applied. Simulated pollen assemblages derived from pollen dispersal modelling were then statistically compared with the fossil assemblages to find the best fit, and hence the most feasible, landscapes for each time slice. By considering the resulting series of palaeoecological-maps in terms of the processes that may have caused the changes through time, a conceptual model of past landscape change at Abernethy nature reserve is suggested (chapter 7).

Results

The major outputs from the project and their contribution to the understanding of the long-term dynamics of the reserve are summarised here.

The Prentice-Sugita model of pollen dispersal and deposition (Prentice, 1985; Sugita 1993, 1994) was successfully validated for major taxa in Caledonian pine forest, so it was deemed suitable for use in the landscape reconstruction process (chapter 4). Palaeoecological records were obtained from seven cores around the reserve. The location and size of the basins chosen allowed a finer scale study of regional and local vegetation change than has so far taken place. Combined with previous published work, this has contributed to the understanding of forest composition, heathland development and the possible effects of climate changes since 8900 cal. BP (8000 BP). New information relating to tephra deposition and its possible effects on vegetation development has been obtained. The first long-term fire history was produced for the reserve, and from this it was inferred that the first of two major periods of increased fire frequency and/or intensity occurred around 7500 cal. BP (6500 BP), which appears to have been associated with one of two phases of heathland development.

It was suggested that forest composition remained relatively unchanged around the reserve until *c.* 5700 cal. BP (5000 BP). It was not possible to determine whether the 'pine decline' manifested itself across the reserve, but at several sites short-lived disturbances affecting the dominant tree taxa seem to have occurred around 4260 cal. BP. These may record localised short-lived changes related to tephra deposition. Charcoal records suggest that a second

widespread period of increased fire frequency and/or intensity began *c.* 3200 cal. BP (3000 BP), with the start of dynamic cycles of heathland formation. Periods where burning subsequently decreased were identified across several sites and it was suggested that these were related to wet shifts in the climate.

Using a simulation approach, it was possible to compare simulated pollen assemblages for many possible landscapes with fossil pollen assemblages. The best matches were used for the reconstruction of three time slices and give the best indication yet of the proportions of different vegetation communities that may have occurred in the past (see chapter 7). The reconstruction was used to infer that the area of pine forest in the 15 km x 15 km study area (and presumably beyond) decreased from *c.* 80% to 60% between 6400 and 4260 cal. BP, then decreased by half again to *c.* 30% by 2150 cal. BP.

Since then, the pollen records suggest that a similar rate of decline has continued, with a further decline in *Pinus* over the past few hundred years, leaving just 15% of the study area currently forested. The pollen records and reconstruction suggest that the forest increased in diversity between 6400 cal. BP and 4260 cal. BP, with an increase in the broad-leaved component. It was suggested that this related to early human clearance gaps, which were of sufficient frequency and duration to produce new niches that were colonised by broadleaved species (see Tipping *et al.*, 1999). For birch/hazel woodland, the reconstruction suggests that cover at 4260 cal. BP was greater than that of 6400 cal. BP, but has subsequently declined from 5% in 2150 cal. BP to less than 0.5% today. The fossil pollen records indicate that this decline has taken place in the very recent past, probably over the past few hundred years.

The reconstruction suggests that from a landscape that was still mainly forested by 4260 cal. BP, a dramatic transition of forest to heathland and blanket bog, particularly on higher ground, took place between 4260 cal. BP and 2150 cal. BP. It is hypothesised that the scale of the transformation, and its links to altitude, was such that a combination of human activity (grazing, burning and clearance) and climatic deterioration was responsible. Since 2150 cal. BP, it appears that heath and blanket bog cover has continued to increase into recent times and the reconstruction supports the idea advanced in chapter 7 that this continued to occur primarily in higher altitude areas.

Implications for management

Conservation evaluation

Conservation decision-making in the UK is usually based on site evaluation adopting criteria such as those of the Joint Nature Conservation Committee (JNCC), as detailed by Ratcliffe (1977) (Hirons *et al.*, 1995). Of these criteria, Birks (1996) proposes that the primary contribution of palaeoecology to conservation evaluation is in the assessment of naturalness, fragility and the conservation status of rare species, and that it can also contribute to the development of a factual basis for ecosystem enhancement or restoration. Palaeoecology may also have useful contributions to make in relation to the recorded history and potential value of a site. The existence of a long recorded scientific history can add to the intrinsic value of a site (Ratcliffe, 1977). Abernethy nature reserve has been the focus of a number of palaeoecological studies, perhaps the most significant being the full Holocene sequence recovered from near Loch Garten, which was used to reconstruct regional vegetation history (Birks and Mathewes, 1978). Palaeoecological studies can also be useful for informing decisions that may improve the potential value of a site, *e.g.* it may provide a longer term context within which to evaluate the restoration potential of damaged systems such as bogs. Here, the results of this project are discussed in relation to the contribution that they can make to the assessment of naturalness, diversity and fragility at Abernethy nature reserve.

Naturalness

As already discussed, the concept of 'naturalness' has a cultural component, which makes it difficult to define. There is a continuum between complete naturalness (probably no longer in existence) and complete unnaturalness, along which concepts of 'naturalness' may be variably positioned (Anderson, 1991). In ecological terms, it can be regarded as the way an ecosystem would have functioned in the absence of humans, which can allow assessment of the degree to which a system has been altered (Anderson, 1991; Peterken, 1996). Palaeoecology can be useful in understanding naturalness beyond the human lifetime perspective, and has been used to establish that modern vegetation communities may not have a long post-glacial history, and that many species that once grew together in the past no longer do so (Watts, 1973; Bennett, 1993; Birks, 1993).

The results of palaeoecological studies at Abernethy Forest indicate the extent of change that has taken place in the forest over the past 8000 years or so, and thus how difficult it is to define the concept of a 'natural' forest. Factors such as climate change and soil development

would have occurred in the forest whether humans had arrived or not. The 'present natural' model concept (Peterken, 1996) as used at Abernethy nature reserve is a useful one as it recognises that such changes will have occurred. It also allows consideration of future changes, the most significant of which over the long-term is probably climate change (Broadmeadow, 2002).

The palaeoecological records from this study suggest that the communities present in the forest today do not, on the whole, have a long history and the current form of much of the forest is probably the result of forestry practices over the past few hundred years. In the context of the longer-term dynamics of the reserve, it can be seen that human disturbances have had an important role in the development of a more open landscape, but that the forest that remained retained its broad-leaved component. It is only relatively recently that this has been severely reduced, leaving the current forest dominated by *Pinus* more so than at any time in its development.

As a result, the current mix of species cannot be regarded as natural, so in the context of restoration should not be used as a basis for decisions related to planting or management to encourage regeneration of particular species. As Tipping (1999) argues, if what remains is not a reflection of past woodland, there is a danger of serious underestimation of the diversity of the original woodland. However, as the palaeoecological perspective suggests that losses in forest diversity are relatively recent, there is a strong possibility that restorative action can be taken (*sensu* Tipping *et al.*, 1999). At Abernethy nature reserve, this could involve the creation of gaps in areas likely to be colonised by existing broad-leaved species, in particular *Betula* and *Alnus*, or possibly re-introduction of trees from native stock into appropriate areas.

Diversity

Diversity can refer to species, community or habitat diversity (Margules and Usher, 1981). Some habitats of high conservation value, such as Caledonian pine forest, may have relatively few species but a high proportion of these will be rare or endemic. Diversity of habitat may arise from a variety of physical features giving rise to a wide variety of plant communities, as is the case at Abernethy nature reserve (Ratcliffe, 1977).

At Abernethy, this study suggests that human clearances led to increased forest diversity, possibly through gap creation that allowed colonisation by broad-leaved species (see Tipping

et al., 1994). It could be argued that early human activity in the forest should be regarded as interference or disturbance rather than clearance as the latter more alteration than may actually have occurred (Tipping, 1994). Birks (1993, 1996) emphasises that many, if not all, present landscapes have developed in close association with human activity, and this is important to bear in mind to encourage a more balanced view of interventionist approaches in the management of the present day 'natural' pine forest. Such interventions may be designed to increase diversity through mimicking 'natural' processes (Peterken, 1996) but where this involves removal of trees, negative public perception can inhibit the development of scientifically based conservation policy and practice (*sensu* Rackham, 1998).

The recent decline in *Betula* suggests that there is a strong case for actively increasing the amount of birch in the forest, which could be carried out on a trial basis by gap creation in locations near to existing *Betula* populations and/or planting saplings reared from native stocks then allowing for natural spread (Peterken, 1996). The spatial resolution at which this project operated meant it was not possible to tell whether or not birch occurred as stands or within a mixed canopy, so any re-introduction programme would need careful design, appropriate site selection and close monitoring. It was also not possible to make inferences about the former presence of other taxa that are less visible in the pollen record, *e.g. Juniperus, Populus, Sorbus* and *Vaccinium*; a higher pollen count would have revealed more rare taxa. The potential exists for *Betula* to be returned to its former levels within the forest if it is assumed that the influence of climate change has not increased greatly over the past few hundred years. Re-introduction of *Corylus* would be more problematic as this would probably require soil alteration (Peterken, 1996).

Fragility

Fragility, like naturalness, is a difficult concept to define. Ratcliffe (1977) suggests that it reflects the sensitivity of habitats, communities and species to environmental change and involves a combination of intrinsic and extrinsic factors. It is not possible to measure fragility directly but an idea of ecosystem sensitivity to change or disturbance can be inferred from studying system responses. This needs a long-term approach, and many palaeoecological studies have attempted to detect impacts on ecosystems of factors such as climate, fire and human activity (*e.g.* Clark, 1988b, 1989; Donnegan *et al.*, 2001; Keller *et al.*, 2002; Froyd, 2006). Ecosystem responses to change or disturbance will operate at a range of scales, and whether or not a return to apparent 'equilibrium' takes place will depend

on the scale at which observation takes place (Weins, 1989). In palaeoecology, this will relate to the spatial and temporal resolution of the sampling.

In this thesis, ecosystem response to change was evaluated at a broad, long-term scale. The relationship between heathland development and changes in fire regime was apparent throughout the study area. A marked change to a more intense, frequent pattern of burning was inferred for the period following 4300 cal. BP (3800 BP) followed by a decrease to low levels of activity over the past few hundred years. It is possible to infer a fire regime periodicity of approximately 1000 years, with three cycles having occurred over the last 3800 years. These may be climate-modulated responses, but in the upper sections of all cores low levels of charcoal appear to relate to recent anthropogenic fire-suppression. The pollen record suggests that, between cycles, *Calluna* abundance has become successively greater, which suggests that an increased fire regime may be justified in order to decelerate what may be an irreversible process of heathland formation and encourage forest regeneration. However, finer resolution sampling would be required to investigate this further.

Approaches to restoration

At Abernethy nature reserve, one conservation aim is to restore forest habitats to all areas below the present day tree line where trees may once have been a natural component (Taylor, 2000). Past climate changes mean that the species composition and extent of past stages in forest development are not suitable models for restoration, which raises the question how a restoration model should be decided upon. If a 'present natural' landscape is the goal (*sensu* Peterken, 1996), the importance of understanding long-term processes becomes apparent. Whilst there may be no control over external threats such as climate change, some processes may be reversible and, as discussed above, the palaeoecological record can enable these to be identified to allow targeting of conservation effort.

In the case of Abernethy nature reserve, many changes have taken place over the past 300 years, and as recent industrialisation appears to have been a major causative factor in these changes, it may be feasible to work towards a model of pre-industrial forest composition and extent (*sensu* Peterken, 1996), although more research would be required upon which to base such a decision. Palaeoecological studies of this period would be useful to understand further the character and dynamics of the landscape at this time, using information from historical records and pollen modelling to test hypotheses relating to ecosystem processes.

An alternative view is that this approach to restoration is not appropriate, as it is too focused on achieving and maintaining a particular state. An ecosystem that is perceivably resilient or stable may actually be at greater risk of loss or damage than an unstable one (Margules and Usher, 1981). Arguably, in the context of future climate change, this approach may now be unrealistic, as it is unlikely that pine forest will ever be in a dynamically stable state in the future (Humphrey, 2006). This gives weight to the idea discussed earlier that conservation of processes, rather than species and habitats, is an important step forward in conservation decision-making, and new ways of maintaining a dynamic system under changing conditions may have to be found.

It was suggested above that the recent decline in *Betula* and other broad-leaved tree species is a recent phenomenon, and that a restored forest should contain a higher proportion of these species. The pollen record suggests that broad-leaved species are at their lowest levels since the forest first became established. In chapter 7, feasible reconstructions of forest composition and extent are suggested for three time slices (Table 7.5). For the most recent, (2150 years ago) it is suggested that around 10% of the total forest cover that remained comprised birch/hazel, a further 10% was mixed pine/birch/hazel woodland and around three quarters of the total woodland area was dominated by pine. This contrasts with the present day, where there is only 1% of birch woodland, 2% of mixed woodland and over 95% woodland dominated by pine.

Although this constitutes a considerable loss of species diversity, it is apparent from pollen records that the abundance of these species has fluctuated in the past, indicating that populations can naturally recover, albeit not necessarily in a human lifetime. This suggests that the active encouragement of *Betula, Alnus* and other broad-leaves are valid propositions for future diversification of native pinewoods. Previous levels of these species could be modelled for the more recent past (*e.g.* the last 500 years) using similar techniques to those demonstrated in chapter 7, provided secure chronologies are available for the time slice approach. Species could be encouraged either by 'acceleration', whereby the growth and performance of planted seedlings is accelerated by scarification to discourage *Calluna*, or by ensuring that species are matched to sites appropriate to their ecologies (Ogilvy *et al.* 2006).

Discussion

This project has attempted to combine traditional palaeoecological techniques with novel methods of landscape reconstruction based on pollen dispersal modelling. An overview of

long-term vegetation dynamics at the reserve-scale has been obtained, and demonstrates the diversity of vegetation development in different locations over time.

The potential of pollen dispersal modelling techniques has also been demonstrated. The use of pollen dispersal models in past landscape reconstruction offers a far more dynamic approach than more traditional approaches such as the modern analogue technique, as it allows modelling and testing of parameters such as spatial patterning, structure and patch size of vegetation (*e.g.* Sugita *et al.*, 1999). However, the size of basins available in the landscape will determine the spatial resolution at which the landscape can eventually be reconstructed, and in many cases this will be restricted (Sugita, 1994; Bunting *et al.*, submitted). Some important model parameters still need to be better characterised. Whilst topographical effects can now be modelled during the process of landscape scenario creation, an important next step will be to be able to incorporate possible topographic influences on pollen dispersal mechanisms; it is already possible to apply windroses (Bunting and Middleton, 2005) but as yet there is no way of investigating factors such as edge effects whereby trees exposed to more light may have increased pollen productivity, combined with more effective entrainment of pollen by the wind.

The landscape scenarios are themselves a useful contribution to debate on 'natural' state of studied area and provide insight into the range of landscape patterns that can produce similar pollen signals for a variety of scales and basin types. It may not always be possible to 'retrodict' the particular spatial properties of the landscape, but in many cases it is useful to be able to eliminate landscape scenarios that do not fit with the pollen evidence. Such findings could contribute to debates on contentious issues such as the former extent of the Caledonian pine forest, *i.e.* whether an 'old wood of Caledon' or less extensive pine-dominated woodland existed in the past, as argued by *e.g.* Breeze (1992) and Tipping *et al.* (1994). This could have important implications for future forest conservation and restoration policy and practice.

Some limitations of the Prentice-Sugita model (Prentice, 1985; Sugita, 1993, 1994) were discussed in chapter 4, but briefly, there is a continued need to refine estimated of important parameters such as pollen productivity, and to further validate the model for a wider range of cultural landscapes. When applied to reconstruction, there is an assumption that climatic conditions would have had similar effects on pollen production, dispersal and deposition in the past as they do today, but unfortunately this is untestable. Parameters such as wind speed

and pollen productivity can be varied, however, to provide insight into the extent to which such factors may affect the pollen signal.

Major advances in pollen analysis theory (Parsons and Prentice, 1981; Prentice and Parsons, 1983; Prentice, 1985; Sugita 1993, 1994) allow the relevant source area of pollen (RSAP) to be quantified for patchy vegetation. This allows more flexibility when comparing sites of different types or sizes as allowances for variations in RSAP can confidently be made. It is now possible to use the Prentice-Sugita pollen dispersal model with real and hypothetical data since the recent development of the HUMPOL software suite (Middleton and Bunting, 2004; Bunting and Middleton, 2005). There will always be limitations to the types of questions palaeoecology can address because of factors such as the availability of palaeoecological records and the poor survival of pollen or macrofossils for particular species. For example, it is difficult to make quantitative estimates of the past presence of trees and shrubs such as *Ilex aquifolium*, *Juniperus*, *Salix* and *Populus tremula* that tend to be under-represented in the pollen record. However, palaeoecology can now operate at spatial and temporal scales that can contribute to the development of strategies for dealing with ecological and cultural landscape problems, increasing knowledge and challenging assumptions about the way landscapes may have developed.

Future work

This work has provided a useful framework within which to consider more specific ecological questions for Caledonian pine forest involving smaller scale patterns and processes than were investigated in this study. Such questions might relate to stand-scale dynamics (*e.g.* bog margin fluctuations, size and persistence of forest patchiness; detection of small scale variations in human activities such as burning and clearance). This would require pollen data that is both temporally and spatially precise (*e.g.* high resolution sampling from a network of forest hollows or small lakes). Such information would be of direct relevance to ecological questions at the community-scale and would allow testing of hypotheses relating to contemporary vegetation processes (Birks, 1993).

Now that reconstructions of past landscapes can be tested with palaeoecological data, this may enhance their credibility for application to practical conservation where they can be applied to forecast future ecosystem responses (Birks, 1996). The pollen modelling approach could also be used to calibrate a predictive tool for future scenarios relating to climate change. This could be achieved by creating a range of possible landscapes that are designed

to reflect past conditions that have already been modelled by other means (*e.g.* identification of palaeoclimatic wet shifts using macrofossils and testate amoebae). Provided secure chronologies are available, fossil pollen records for which data from independent palaeoclimate proxies is also available could be used to test the landscapes. If the calibration is successful, predictions of possible future effects of climate change on ecosystems should be possible.

There is also further scope for testing the application of the modelling approach to fossil pollen by using historical maps from the Abernethy Forest area to generate past vegetation maps for testing against suitably well-dated pollen profiles from the last 350 years. This approach has been successfully applied in Denmark using lake profiles (Nielsen, 2003, 2004).

Conclusion

This project set out to gain a better understanding of long-term vegetation dynamics in Caledonian pine forest, focusing on investigating changes in forest openness and composition, heathland development, fire history and evidence for human activity.

Important new information on spatial variability and changes in forest diversity, heathland cycling, and the human induced fire history at the landscape scale is presented here. The palaeoecological records have provided on the first long-term fire history for Abernethy nature reserve and have given some insight into individual site histories and how these relate to changes in regional vegetation over the past *c.*8000 years.

The secondary aim was to evaluate novel approaches to landscape reconstruction based on pollen dispersal modelling. The Prentice-Sugita model was found to have performed well for major taxa in this landscape (*Pinus*, *Betula*, *Calluna* and Poaceae/Cyperaceae) using available pollen productivity estimates. Additional surface sample data with a wider range of proportions of some major taxa *e.g. Betula*, would have provided more robust predictions with respect to these taxa. Also, surface samples from a wider range of communities with uncommon taxa (*e.g. Salix*, *Corylus* and *Alnus*) may have allowed less common pollen types be modelled more effectively; this would require sampling outside of the Abernethy Forest area.

The potential of using the model in conjunction with palaeoecological records to identify feasible landscape reconstructions for past time slices was successfully demonstrated,

although the availability of more sites or a secure chronology would have allowed more rigorous testing for the 2150 cal. BP time slice. The robustness of the results would also have been improved if the full Multiple Scenario Approach were used to enable testing of larger numbers of possible landscapes. However, the reconstruction has shown that past landscapes relating to specific hypotheses can be created using more objective methods than has previously been possible, and that they can be tested against palaeoecological records. This is a contribution to what Davis (1994) regards as the future of palaeoecological modelling.

If developments in fine resolution palaeoecology and landscape reconstruction are to address the most important issues in nature conservation and ecological management however, palaeoecologists must remain aware of advances in ecological fields (May, 1994). Conversely, as Willis (1993, 1994) points out, palaeoecology is still absent from many long-term ecology debates, so a need remains for closer collaboration and merging of the two disciplines in the future. It is a widely cited truism that the 'past is the key to the present' and, if the general principles under which ecological processes operate are constant over time, then the present, taken in the context of the past, could be used as a key to the future. This thesis demonstrates the importance of understanding long-term dynamics of Caledonian pine forest and the potential contribution that palaeoecology can make to the future management of important cultural landscapes in a changing world.

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Appendix 1a.

Tephra geochemistry: electron microprobe determined abundance of ten major elements in tephra shards from Abernethy Forest.

North Abernethy 95 cm

Na_2O	MgO	SiO_2	Al_2O_3	K_2O	FeO	CaO	TiO_2	MnO	P_2O_5	Total
4.82	0.03	69.74	13.37	2.34	3.18	2.05	0.21	0.14	0.05	95.91
4.53	0.01	71.41	12.36	3.82	1.90	1.22	0.09	0.19	-0.05	95.52
3.10	0.02	71.50	12.31	5.54	1.73	1.30	0.06	0.07	0.02	95.66
4.72	0.03	72.84	12.84	3.17	1.92	1.32	0.11	0.09	0.00	97.05
4.55	0.01	73.06	12.68	2.62	1.98	1.24	0.10	0.09	0.03	96.37
3.29	0.04	73.09	12.54	4.81	1.93	1.33	0.11	0.05	-0.17	97.19
4.81	0.03	73.18	12.91	2.84	1.95	1.32	0.15	0.08	0.10	97.36
4.54	0.03	73.32	12.59	3.02	2.02	1.32	0.07	0.08	0.12	97.09
3.35	-0.01	73.33	12.84	2.91	1.96	1.30	0.10	0.08	0.14	96.02
4.68	0.02	73.82	12.72	2.95	1.98	1.34	0.12	0.12	0.03	97.77
4.66	0.00	74.02	12.77	2.81	1.91	1.30	0.14	0.11	-0.02	97.71
4.65	0.01	74.71	13.27	3.14	1.95	1.32	0.12	0.10	0.03	99.31

Carn a'Chnuic 142 cm

Na_2O	MgO	SiO_2	Al_2O_3	K_2O	FeO	CaO	TiO_2	MnO	P_2O_5	Total
5.01	0.00	70.89	13.18	2.67	2.48	1.68	0.17	0.12	-0.03	96.20
0.84	0.04	71.73	12.17	9.21	1.81	1.07	0.11	0.09	0.03	97.10
5.06	0.02	72.37	12.39	2.65	1.89	1.38	0.10	0.02	0.02	95.91
4.61	0.02	72.48	12.74	2.79	1.96	1.29	0.13	0.09	-0.05	96.10
4.77	0.02	72.69	12.53	2.84	1.91	1.38	0.11	0.05	0.09	96.38
4.76	0.03	72.74	12.73	2.86	1.99	1.36	0.10	0.11	0.07	96.74
4.07	0.02	72.85	12.64	4.25	1.87	1.36	0.09	0.06	0.22	97.44
4.55	0.00	73.05	13.09	2.82	1.89	1.30	0.14	0.08	0.02	96.95
4.77	0.02	73.43	12.69	2.93	1.91	1.18	0.11	0.07	0.02	97.13
4.60	0.01	73.78	13.00	2.80	2.02	1.26	0.10	0.09	-0.10	97.65
4.79	0.03	73.89	12.59	2.82	1.95	1.35	0.14	0.18	-0.02	97.73
4.81	0.01	74.04	13.19	2.72	1.95	1.29	0.11	-0.02	0.03	98.14
4.80	0.03	74.05	12.96	3.06	1.95	1.30	0.12	0.06	-0.05	98.33

Appendix 1b

Forest Lodge 123 cm

Na_2O	MgO	SiO_2	Al_2O_3	K_2O	FeO	CaO	TiO_2	MnO	P_2O_5	Total
3.9963	1.3487	66.5766	13.1185	1.4641	6.5161	4.2639	1.1024	0.1299	0.3201	98.8365
4.029	0.7658	69.4848	13.0939	1.7189	4.9551	2.9785	0.7556	0.0516	0.2043	98.0376
4.2791	0.4936	69.814	12.6212	1.8737	4.1409	2.4597	0.5715	0.0954	0.1196	96.4688
3.9942	0.7631	69.9407	12.9463	1.6489	4.6997	3.0902	0.7226	0.1218	0.1704	98.0978
3.8718	0.7466	70.0013	13.0871	1.6764	4.769	2.9458	0.77	0.1591	0.1875	98.2147
4.2456	0.4214	70.3621	12.1684	2.0017	3.6492	2.1556	0.5317	0.1543	0.137	95.827
4.0979	0.6424	70.4141	13.2465	1.8437	4.6067	2.8439	0.7201	0.2113	0.1363	98.7629
3.1644	0.506	70.4749	12.691	1.5754	4.1355	2.5795	0.6416	0.0789	0.12	95.9671
4.1923	0.4418	70.7327	12.4168	2.0827	3.8523	2.1361	0.5505	0.1007	0.0171	96.523
4.1095	0.5755	71.0159	12.7891	1.7615	4.3942	2.7132	0.6064	0.0999	0.1709	98.2359
4.2888	0.5756	71.3211	12.898	1.8312	4.3561	2.6331	0.6591	0.147	0.1195	98.8296
4.3938	0.3957	71.4243	12.3814	1.9676	3.7426	2.3845	0.529	0.0135	0.1029	97.3352
4.6396	0.4046	71.4337	12.4334	2.0301	3.6291	2.3125	0.4935	0.1255	0.1027	97.6048
4.2414	0.4295	72.457	12.601	1.9285	3.6642	2.3319	0.6121	0.0676	0.12	98.453
4.1588	0.408	72.7137	12.5158	1.925	3.6671	2.2385	0.5328	0.131	-0.0515	98.2906
4.2706	0.4419	72.7231	12.7196	2.0175	3.5768	2.225	0.5401	0.1053	0.1543	98.7743
4.1048	0.4309	72.7467	12.3074	1.9937	3.9518	2.2854	0.5656	0.0805	0	98.4669
4.3496	0.4006	72.8618	13.032	1.9932	3.8239	2.3167	0.5957	0.1448	-0.0171	99.5182
4.5016	0.4107	73.2382	12.6057	1.9838	3.5704	2.1308	0.5229	0.1155	0.2231	99.3027
1.2638	0.4011	76.4896	13.0506	2.0768	3.7886	2.2071	0.4808	0.0827	0.1551	99.9962
1.907	0.3386	76.6918	13.2349	1.8818	3.5253	2.0967	0.5445	0.1291	0.1207	100.4704

Loch a'Chnuic 36 cm

Na_2O	MgO	SiO_2	Al_2O_3	K_2O	FeO	CaO	TiO_2	MnO	P_2O_5	Total
9.18	0.00	61.86	22.98	0.22	-0.01	4.81	-0.01	-0.04	0.03	99.09
0.01	0.00	100.55	0.01	0.06	-0.03	0.00	0.01	0.02	-0.02	100.66
0.02	0.01	100.00	-0.02	-0.01	-0.02	-0.02	-0.01	0.03	0.02	100.07
0.00	-0.01	100.28	0.02	0.01	-0.02	-0.01	0.00	0.03	0.02	100.37
0.03	0.01	101.22	-0.04	-0.01	0.01	0.01	-0.01	0.01	0.02	101.30
11.41	-0.01	65.97	19.96	0.08	-0.02	1.18	-0.02	0.01	0.07	98.67
11.74	-0.01	68.13	19.72	0.09	-0.04	0.43	0.01	-0.02	-0.02	100.11
0.02	0.01	97.74	-0.01	0.00	0.01	0.00	0.00	-0.02	0.05	97.83
0.04	0.00	101.54	0.07	0.01	0.01	0.02	0.03	-0.05	0.07	101.80
0.01	0.00	100.04	0.14	-0.01	0.05	-0.01	0.00	-0.02	0.11	100.36
0.01	0.00	100.35	0.02	0.02	0.00	0.01	0.02	0.05	0.00	100.47
0.02	0.01	99.03	0.02	0.01	0.04	0.01	-0.01	0.00	-0.04	99.15
11.05	0.00	66.32	20.59	0.19	-0.01	1.42	-0.03	0.01	0.02	99.60
3.59	0.04	81.44	2.11	0.77	0.06	0.05	0.05	0.05	-0.02	88.17

Appendix 1b cont.
Tore Hill 288 cm

Na_2O	MgO	SiO_2	Al_2O_3	K_2O	FeO	CaO	TiO_2	MnO	P_2O_5	Total
4.81	0.01	71.25	11.75	2.74	1.92	1.20	0.07	0.06	0.07	93.87
4.61	0.02	72.14	12.63	2.87	1.78	1.28	0.10	0.07	-0.07	95.49
4.91	0.02	72.44	12.59	2.80	1.89	1.33	0.10	0.06	-0.03	96.14
4.68	0.01	72.53	12.24	2.88	1.97	1.29	0.10	0.07	-0.02	95.77
4.65	0.01	72.90	12.69	2.79	1.92	1.29	0.11	0.06	-0.03	96.41
4.26	0.02	72.99	12.51	3.83	1.97	1.27	0.07	0.10	0.05	97.08
4.77	0.03	73.32	12.88	2.72	1.81	1.38	0.13	0.13	0.10	97.28
4.97	0.01	73.53	12.82	2.82	1.97	1.29	0.10	0.11	-0.07	97.63
4.77	0.00	73.59	12.99	2.89	1.95	1.38	0.09	0.11	-0.02	97.76
4.69	0.01	73.94	13.32	2.91	2.08	1.26	0.08	0.10	0.05	98.45
3.10	0.00	74.44	12.81	4.36	2.03	1.34	0.12	0.17	0.02	98.38

Forest Lodge 194 cm

Na_2O	MgO	SiO_2	Al_2O_3	K_2O	FeO	CaO	TiO_2	MnO	P_2O_5	Total
4.13	0.03	72.30	12.90	2.72	1.85	1.31	0.11	0.11	0.02	95.48
5.13	0.01	72.39	12.34	2.65	1.89	1.35	0.13	0.03	-0.09	95.91
4.28	0.09	72.46	12.69	2.84	1.80	1.32	0.12	0.09	-0.02	95.69
4.51	0.02	72.73	12.56	2.80	1.78	1.27	0.11	0.07	0.02	95.86
5.15	0.00	72.92	12.55	2.63	1.85	1.35	0.10	0.06	-0.02	96.61
5.01	0.03	72.93	12.64	2.85	2.00	1.38	0.11	0.06	0.03	97.04
5.10	0.00	72.94	12.70	2.80	1.92	1.31	0.14	0.09	0.03	97.04
3.73	0.04	73.12	13.09	2.60	1.90	1.25	0.08	0.05	0.07	95.95
4.87	0.03	73.15	12.80	2.86	2.06	1.24	0.12	0.14	0.07	97.34
4.75	0.03	74.24	13.11	2.65	2.08	1.29	0.10	0.06	-0.03	98.32
3.04	0.00	74.43	13.17	2.89	1.94	1.34	0.10	0.08	0.00	97.00

Appendix 1b cont.
Loch an Spioraid 111 cm

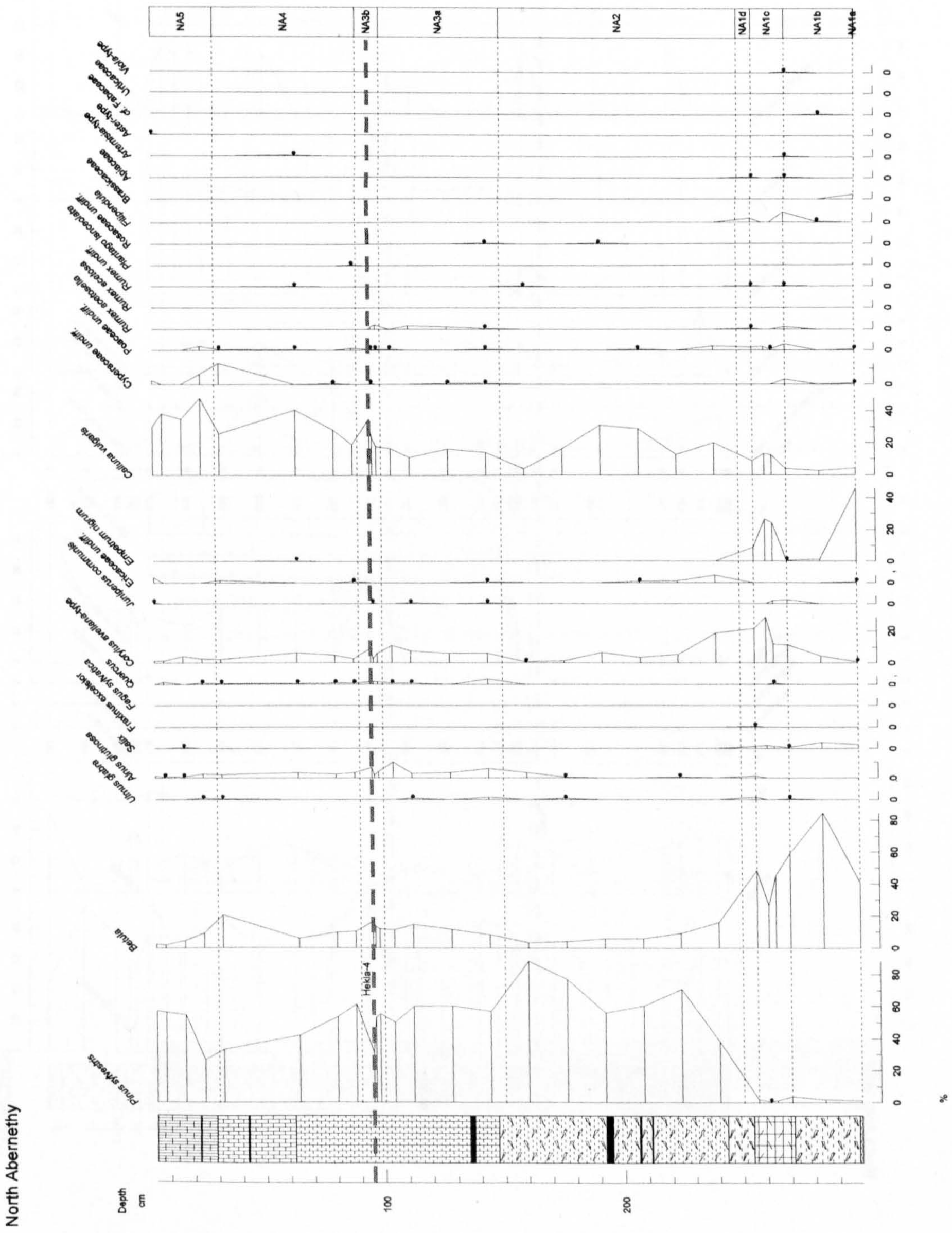
Na_2O	MgO	SiO_2	Al_2O_3	K_2O	FeO	CaO	TiO_2	MnO	P_2O_5	Total
2.40	0.00	70.89	12.17	6.41	1.89	1.21	0.10	0.13	-0.02	95.20
1.41	0.03	71.66	12.08	7.62	1.86	1.34	0.11	0.07	0.03	96.22
4.71	0.03	71.90	12.77	2.80	2.03	1.37	0.10	0.09	-0.03	95.80
3.58	0.05	71.93	12.50	4.47	1.94	1.25	0.13	0.09	0.05	95.98
4.64	0.02	72.65	12.77	2.81	1.92	1.26	0.11	0.10	-0.02	96.28
3.65	0.03	73.34	12.91	4.61	1.95	1.31	0.14	0.02	0.12	98.08
4.60	0.01	73.53	12.86	3.61	1.85	1.27	0.11	0.13	0.07	98.05
4.29	0.01	73.68	12.99	3.48	1.96	1.24	0.12	0.08	0.02	97.87
4.80	0.05	73.98	12.77	2.83	1.92	1.31	0.09	0.05	-0.03	97.80
3.97	0.02	73.99	13.03	4.53	1.86	1.32	0.17	-0.04	-0.09	98.88
3.59	0.02	74.57	12.73	3.06	1.98	1.33	0.09	0.01	0.00	97.38

Faesheallach Burn 151 cm

Na_2O	MgO	SiO_2	Al_2O_3	K_2O	FeO	CaO	TiO_2	MnO	P_2O_5	Total
4.90	0.00	72.26	12.47	2.73	1.88	1.26	0.09	0.07	0.00	95.65
4.77	0.02	72.46	12.49	2.81	2.00	1.31	0.12	0.09	-0.10	96.08
4.74	0.03	72.59	12.77	2.79	1.97	1.32	0.10	0.11	-0.03	96.42
5.03	0.02	73.10	12.62	2.89	1.99	1.29	0.12	0.08	0.09	97.22
4.61	0.03	73.13	12.73	2.65	1.95	1.22	0.16	0.08	0.02	96.58
4.55	0.01	73.19	12.94	2.66	1.92	1.27	0.12	0.03	0.09	96.77
4.56	0.03	73.31	12.75	2.85	1.78	1.28	0.10	0.09	0.10	96.84
4.23	0.01	73.31	12.67	3.77	1.77	1.24	0.07	0.02	0.03	97.13
4.84	0.02	74.03	13.03	2.82	1.97	1.32	0.08	0.08	-0.05	98.18
4.63	0.04	74.28	13.11	3.37	1.86	1.37	0.14	0.13	0.00	98.91
3.51	0.00	74.63	13.04	4.98	2.01	1.26	0.10	0.10	0.09	99.73

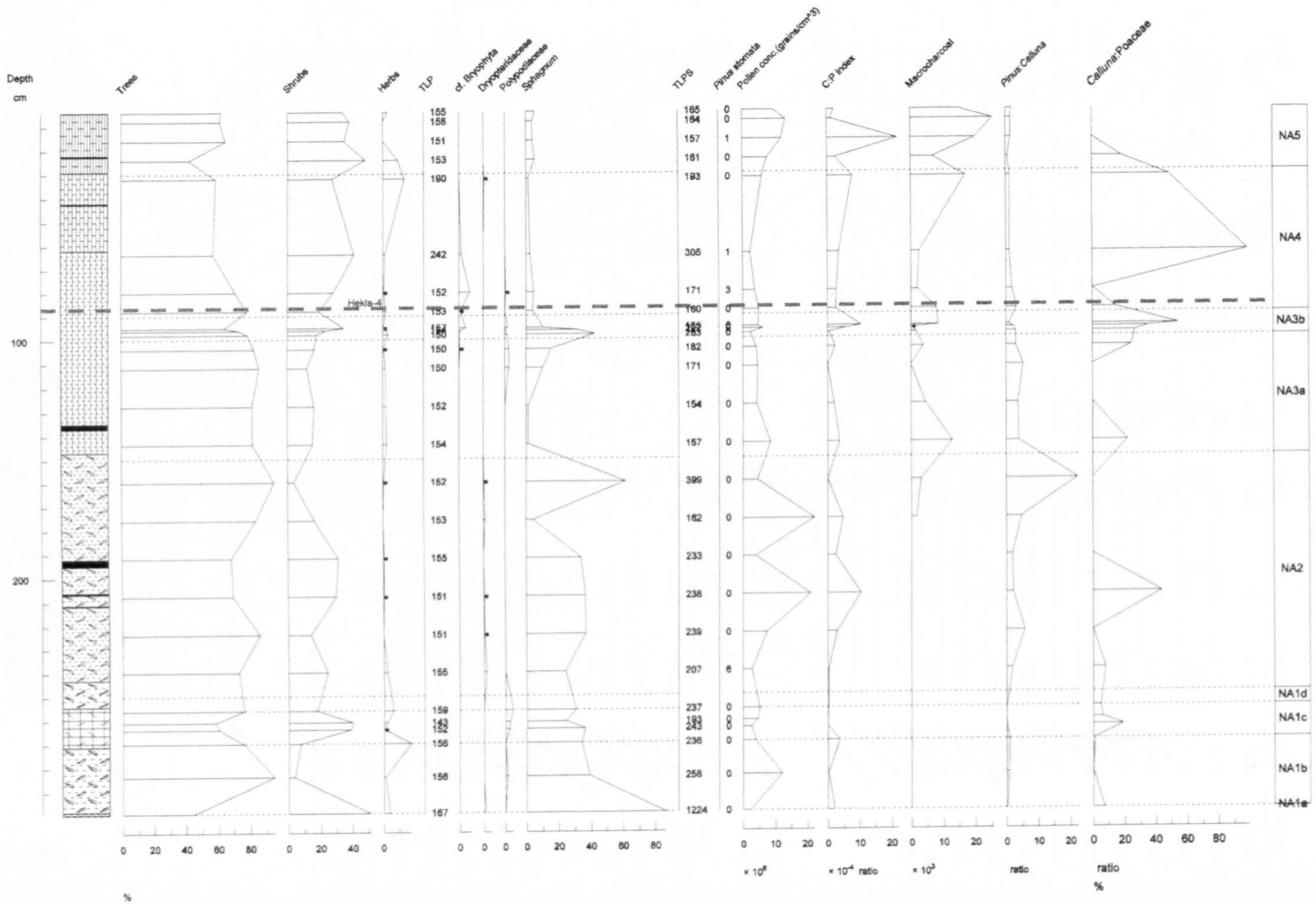
Appendix 2a.

Full pollen diagrams for chapter 5.

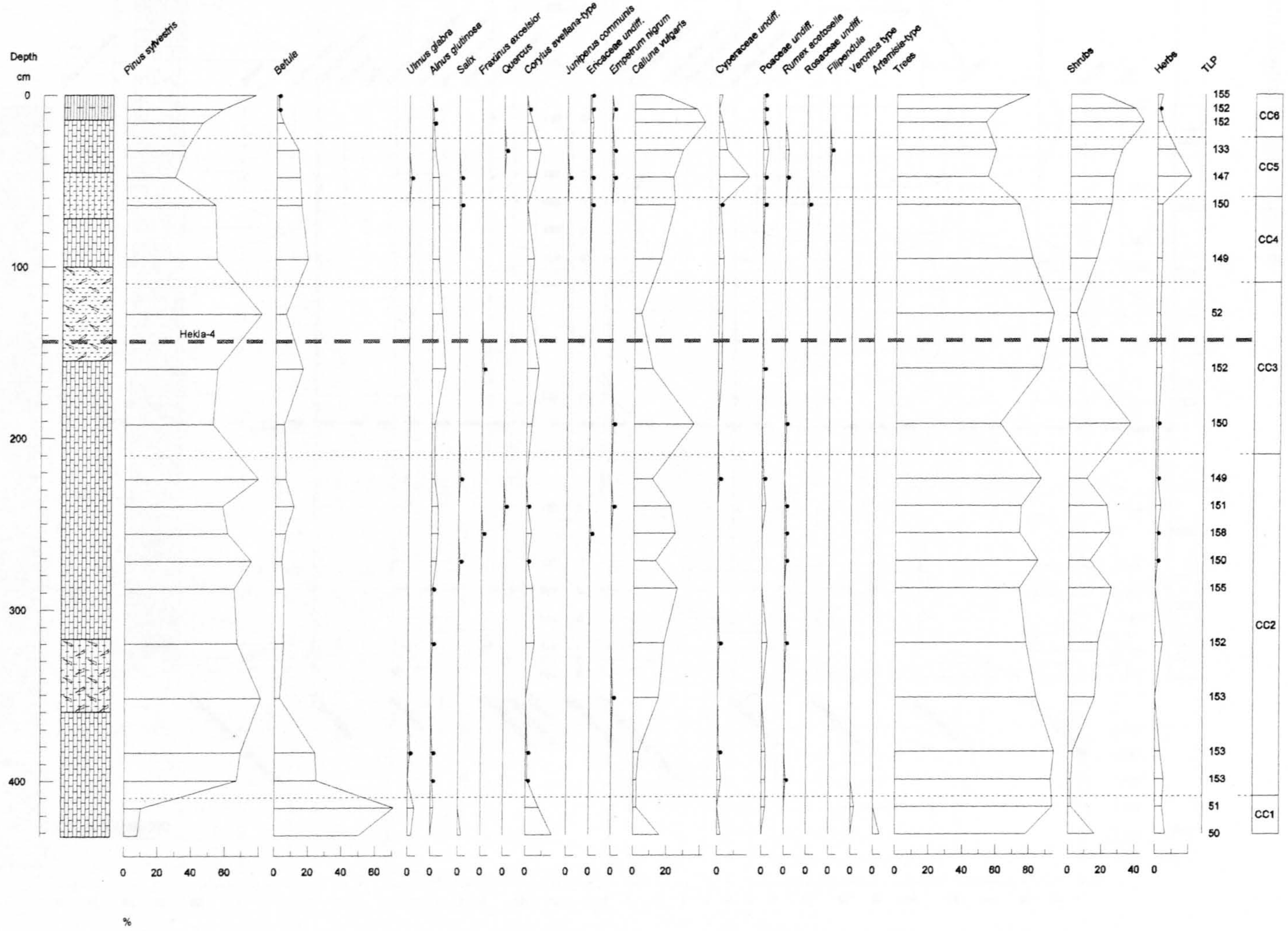


North Abernethy

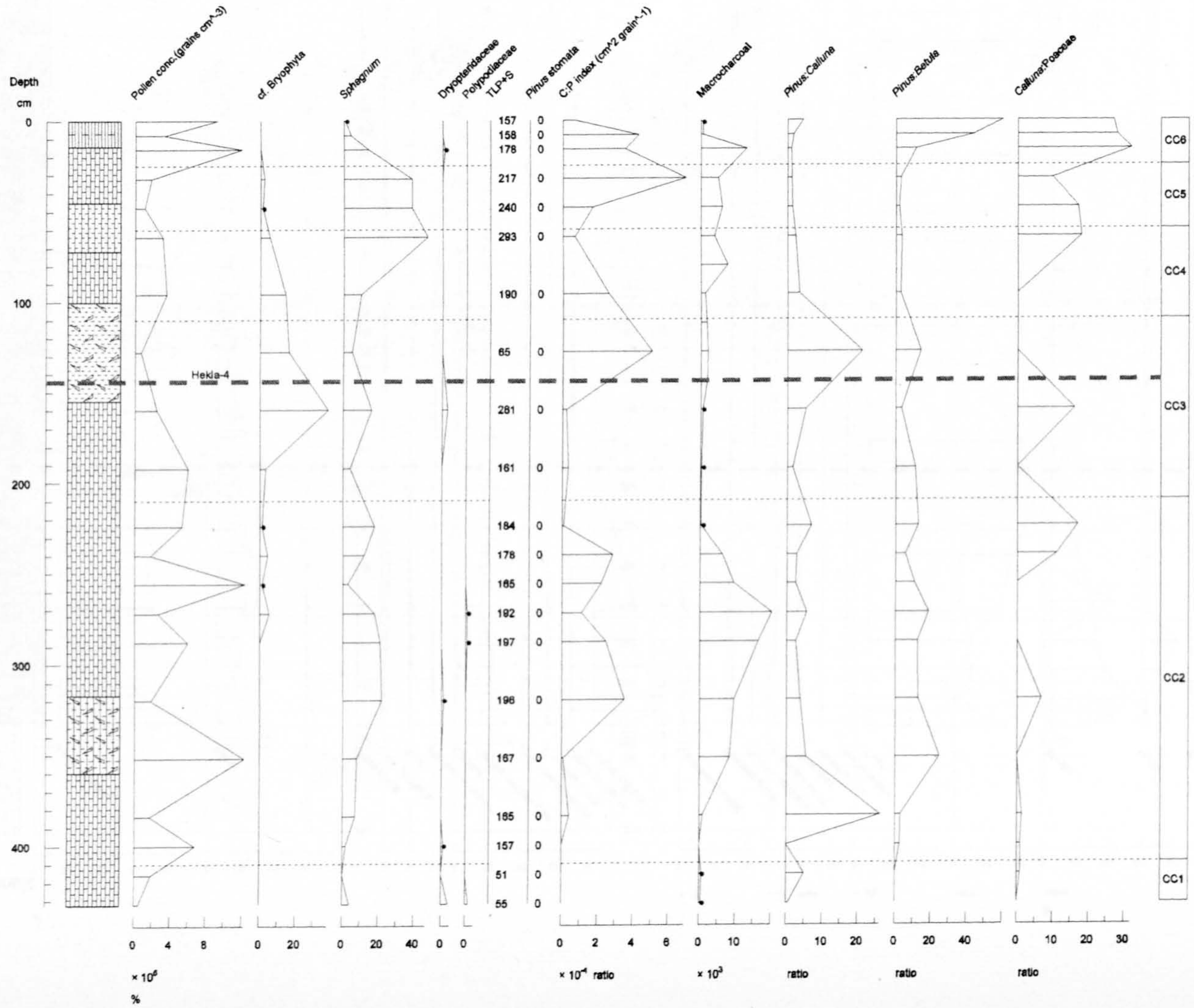
North Abernethy



Carn a'Chnuic

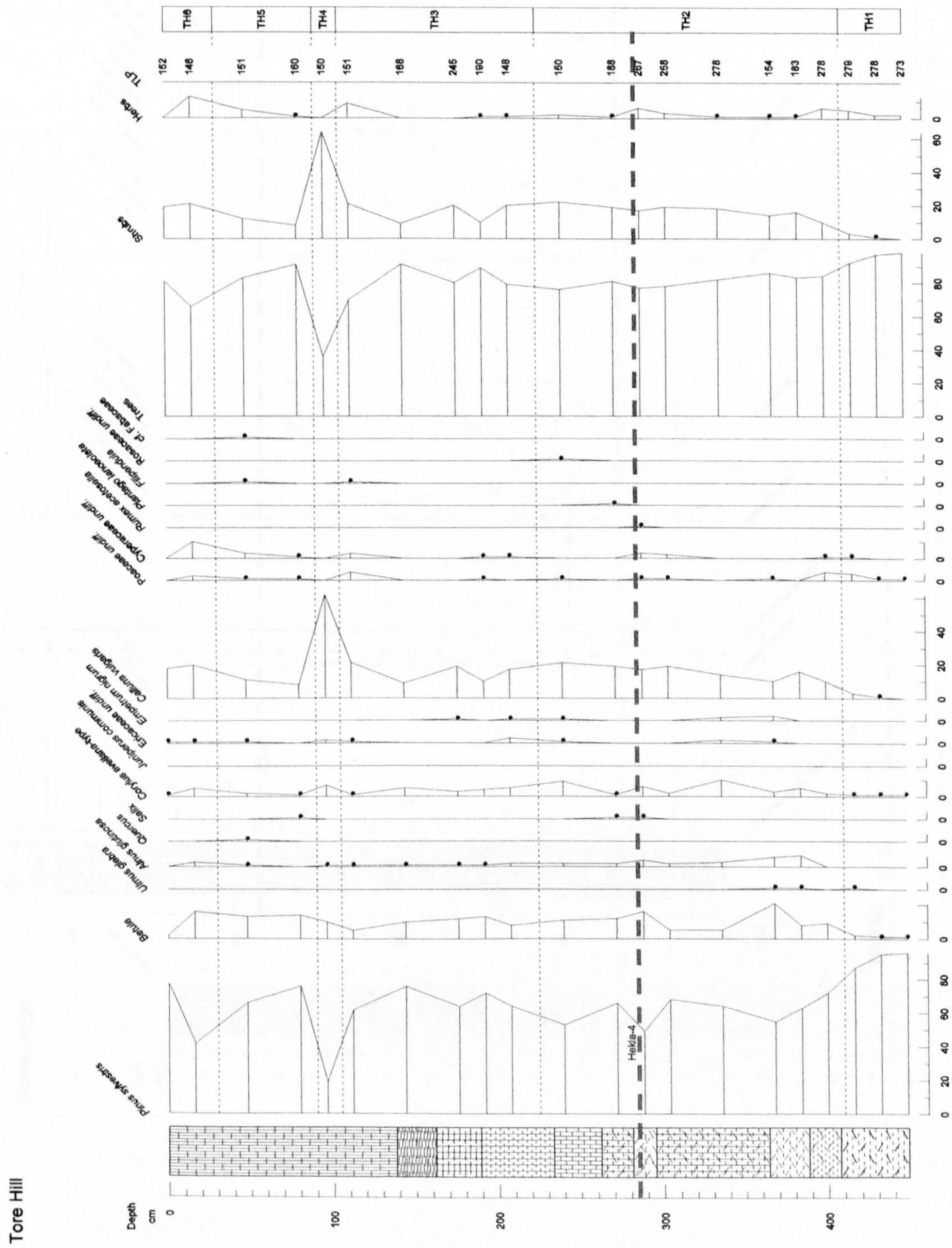


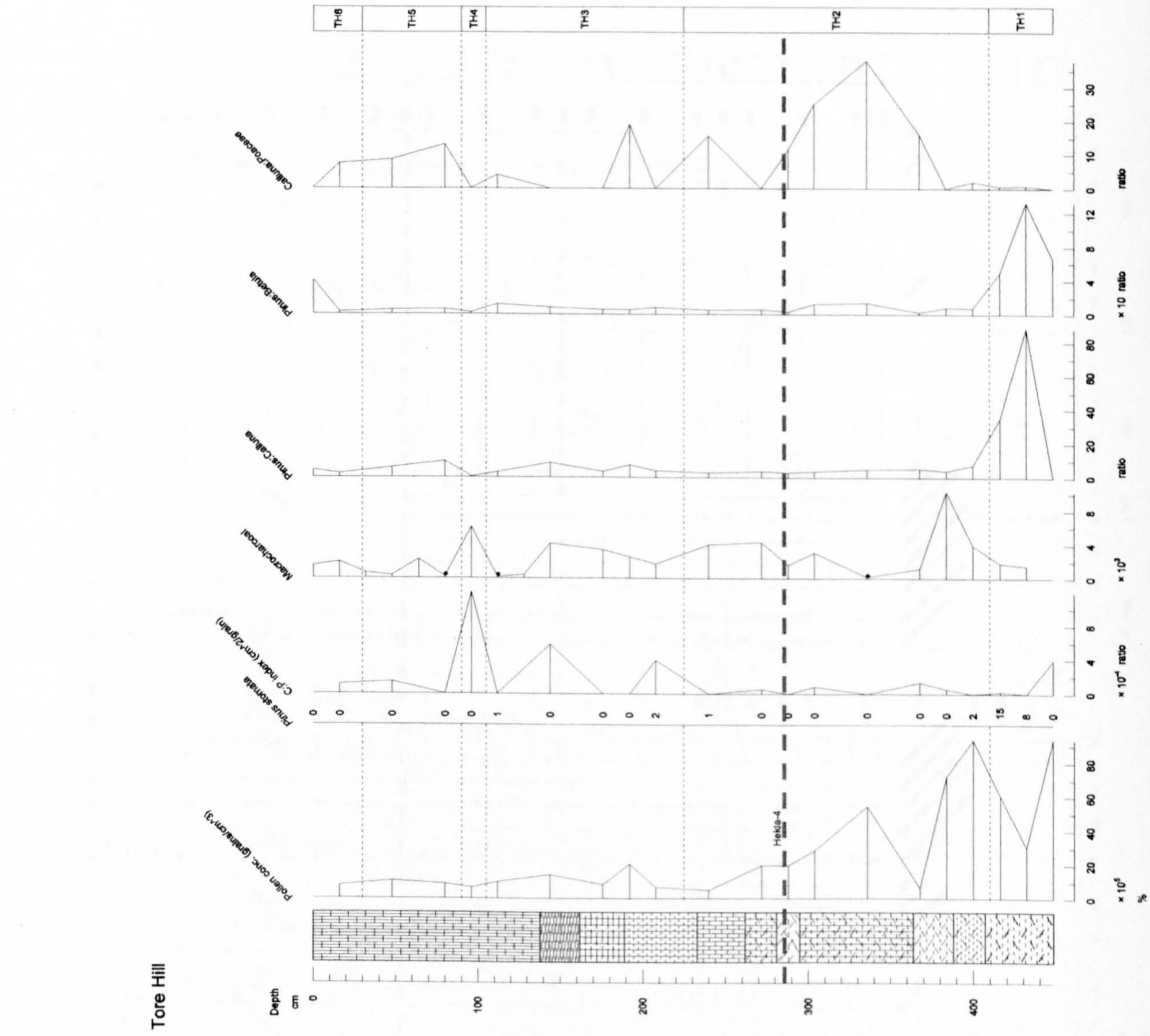
Carn a'Chnuic



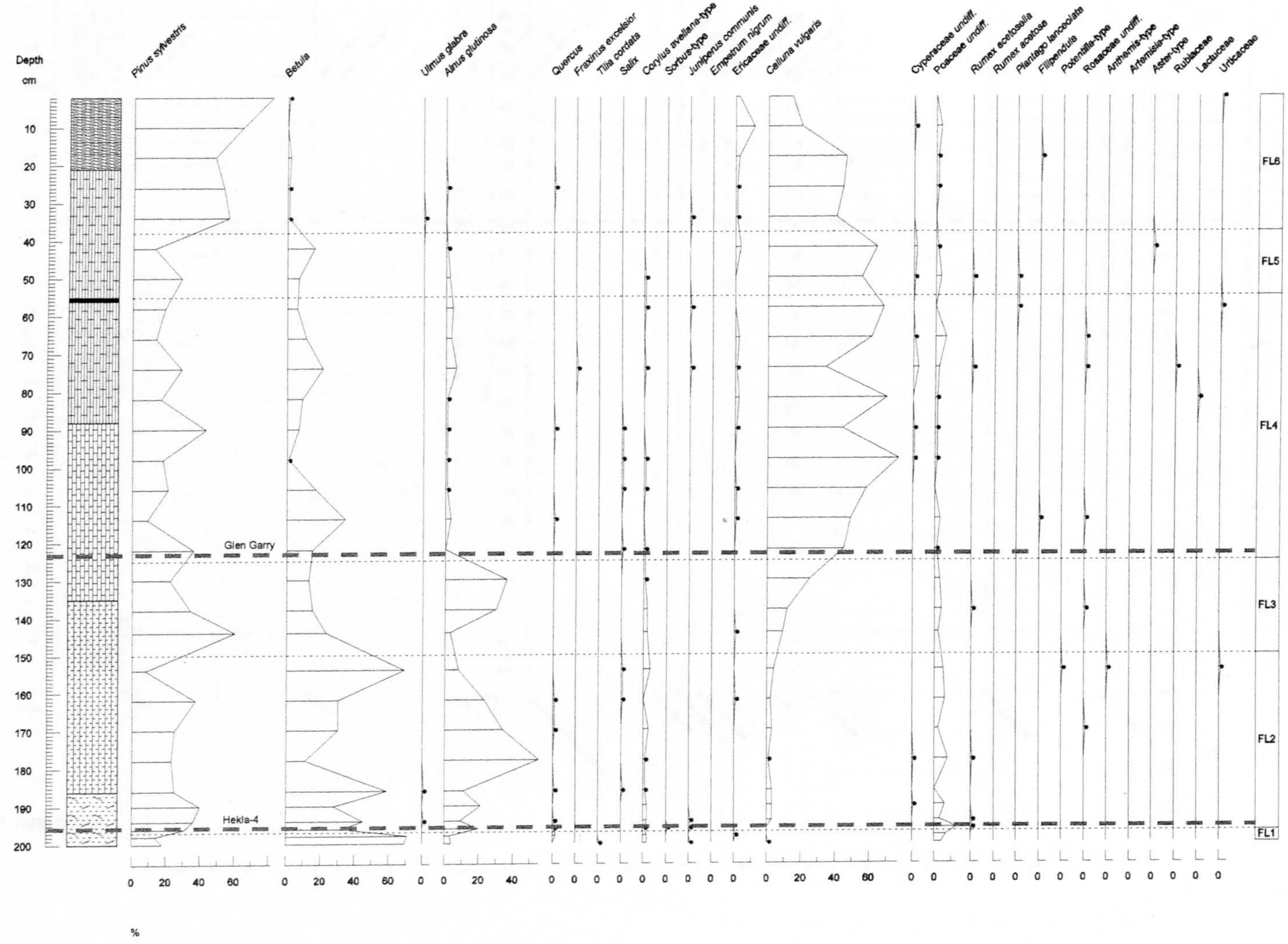
Appendix 2b.

Full pollen diagrams for chapter 6.

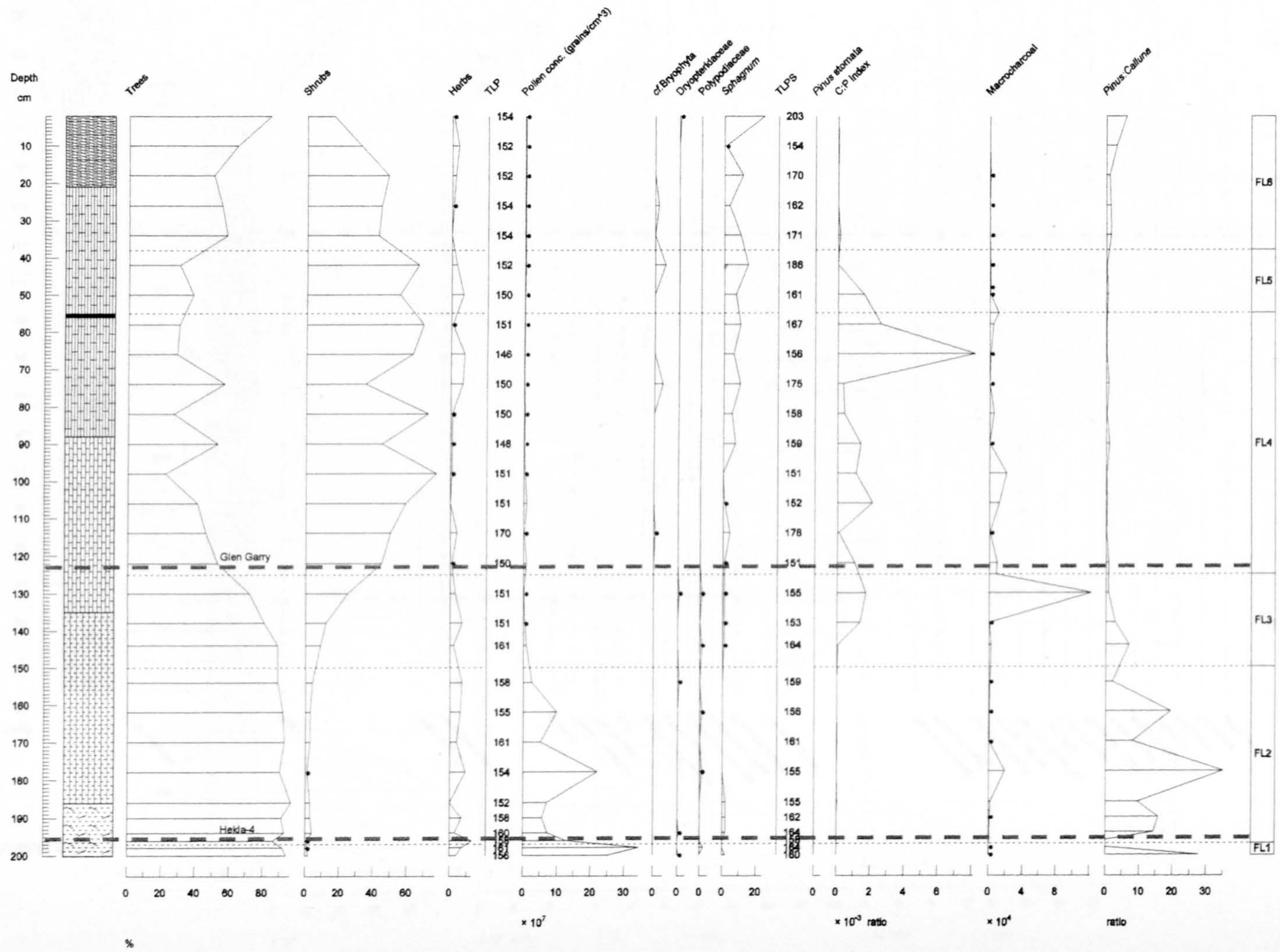



Tore Hill
Depth
cm
0
100
200
300
400
TH-6
TH-5
TH-4
TH-3
TH-2
TH-1
Hekla-4
Pollen conc. (grains/cm^3)
Pinus stomata
C.P. index (cm^2/grain)
Macrocharcoal
Pinus:Calluna
Pinus:Betula
Calluna:Poaceae
%
× 10^5
× 10^4 ratio
× 10^3
ratio
× 10 ratio

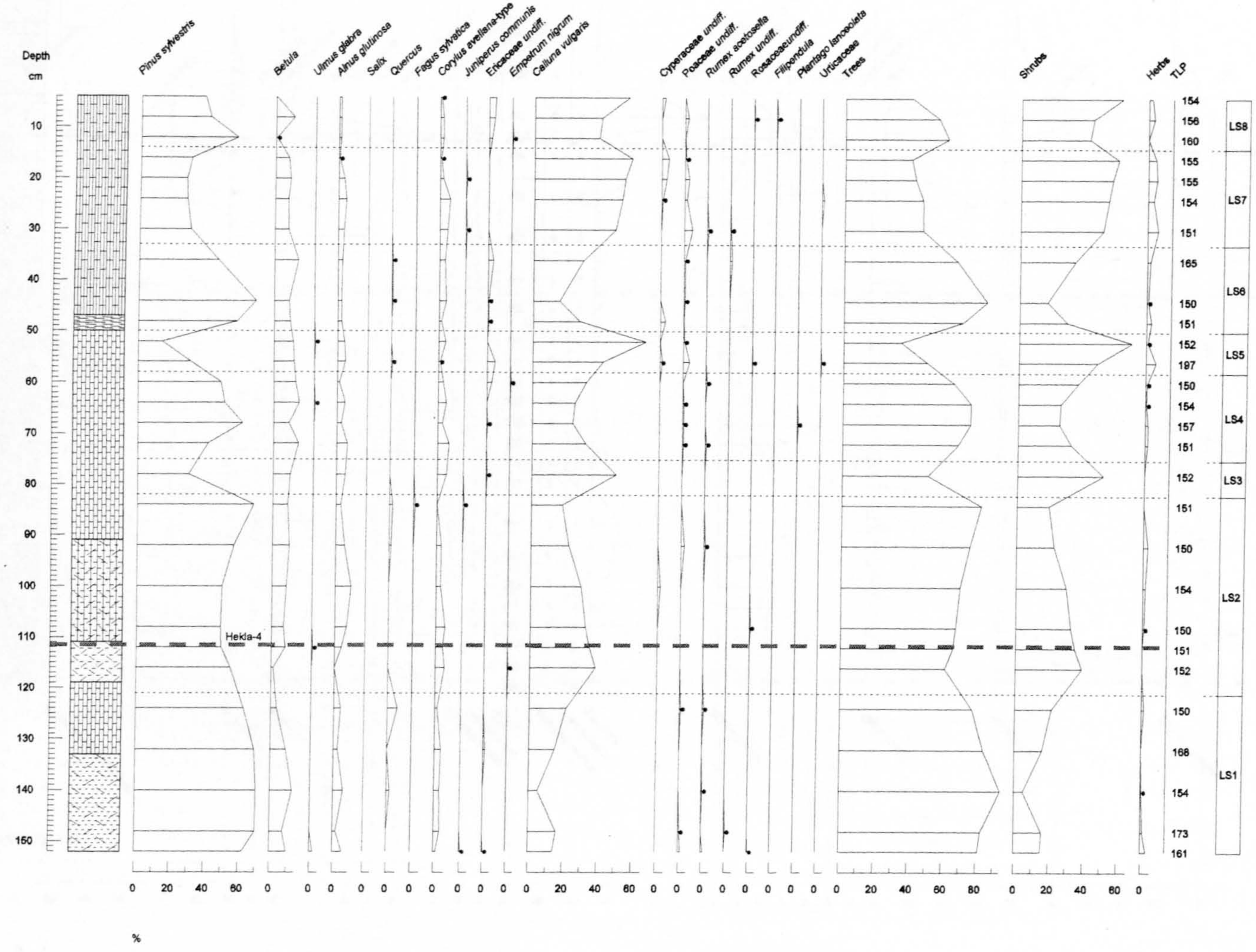
Forest Lodge



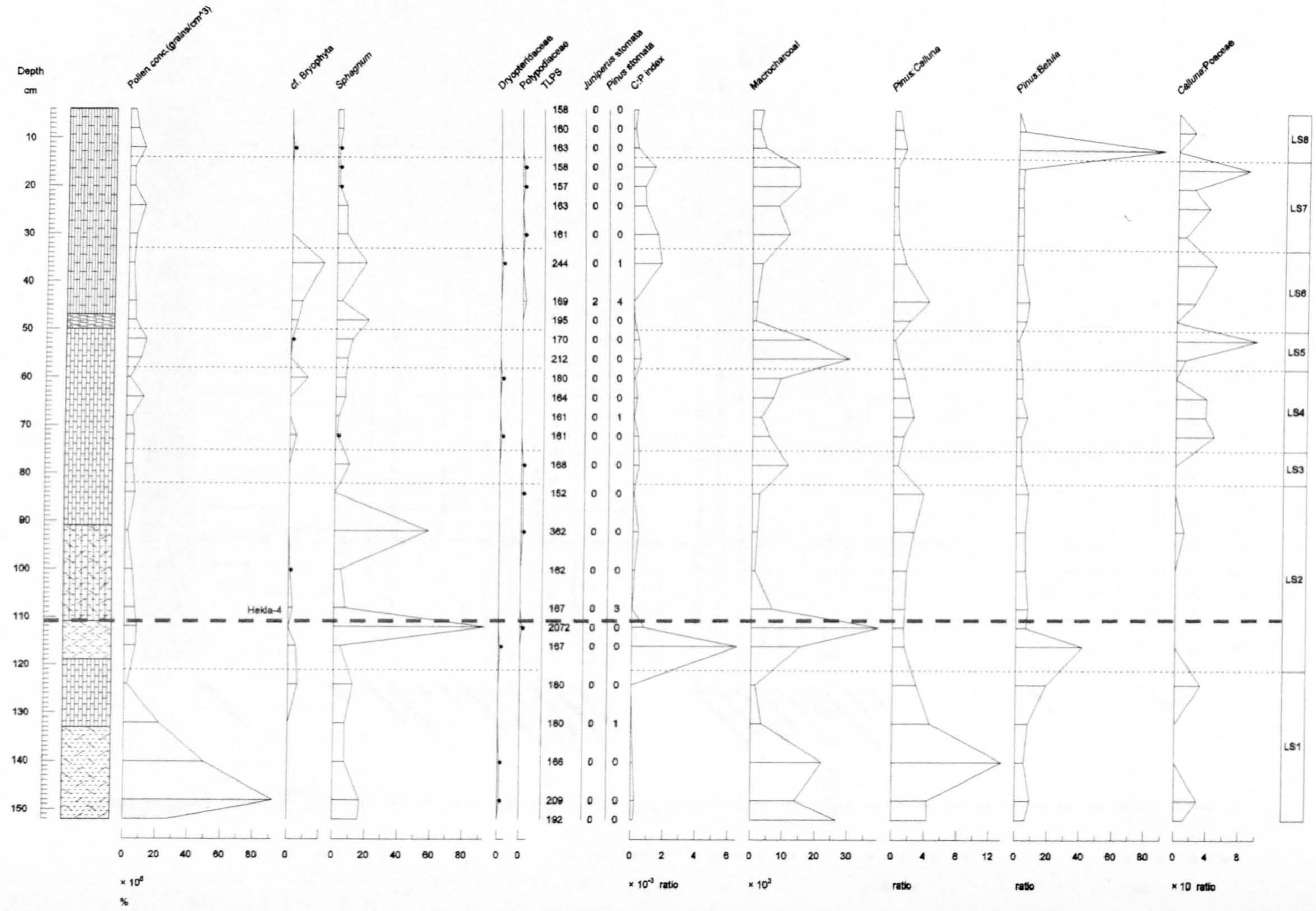
Forest Lodge



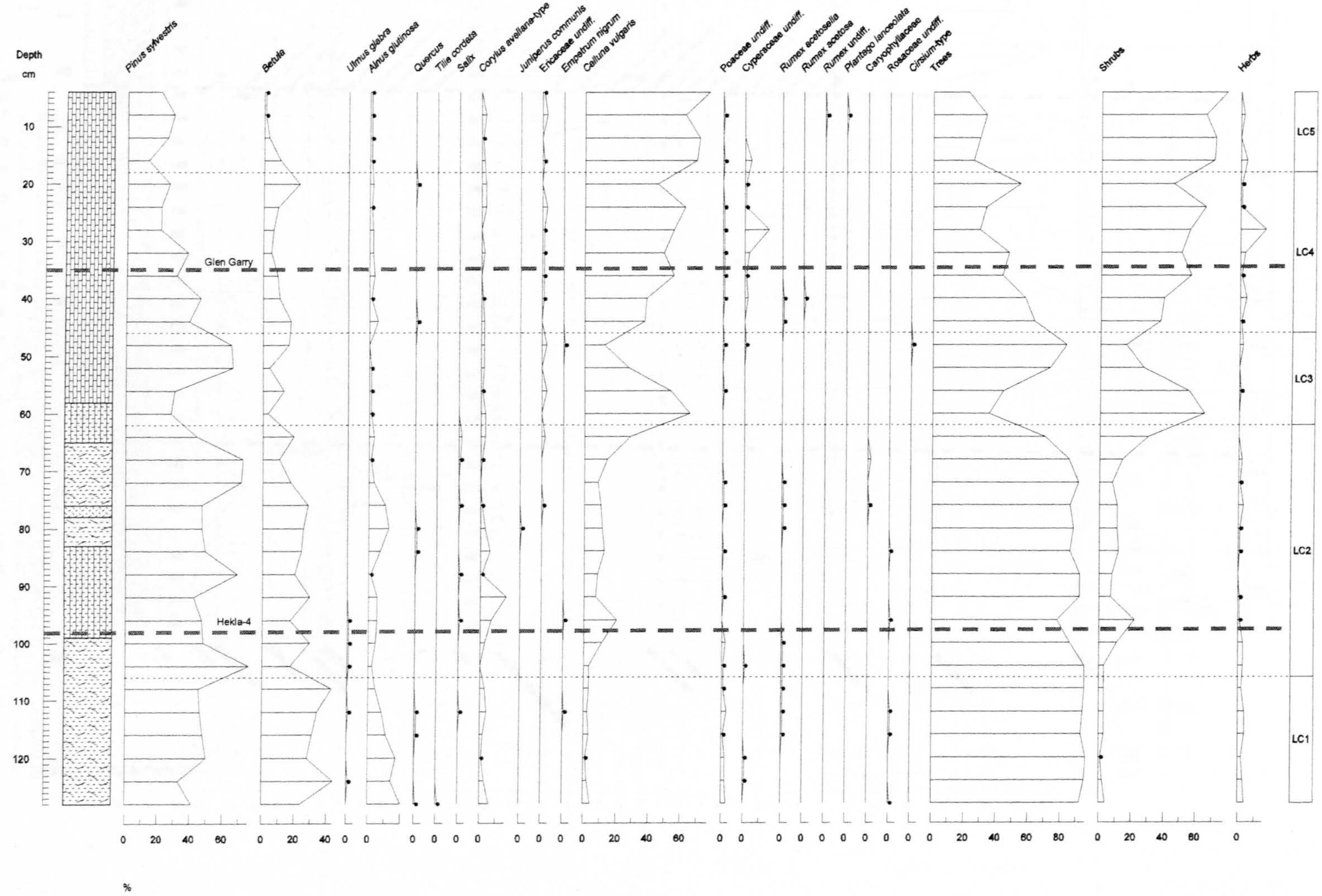
Loch an Spioraid

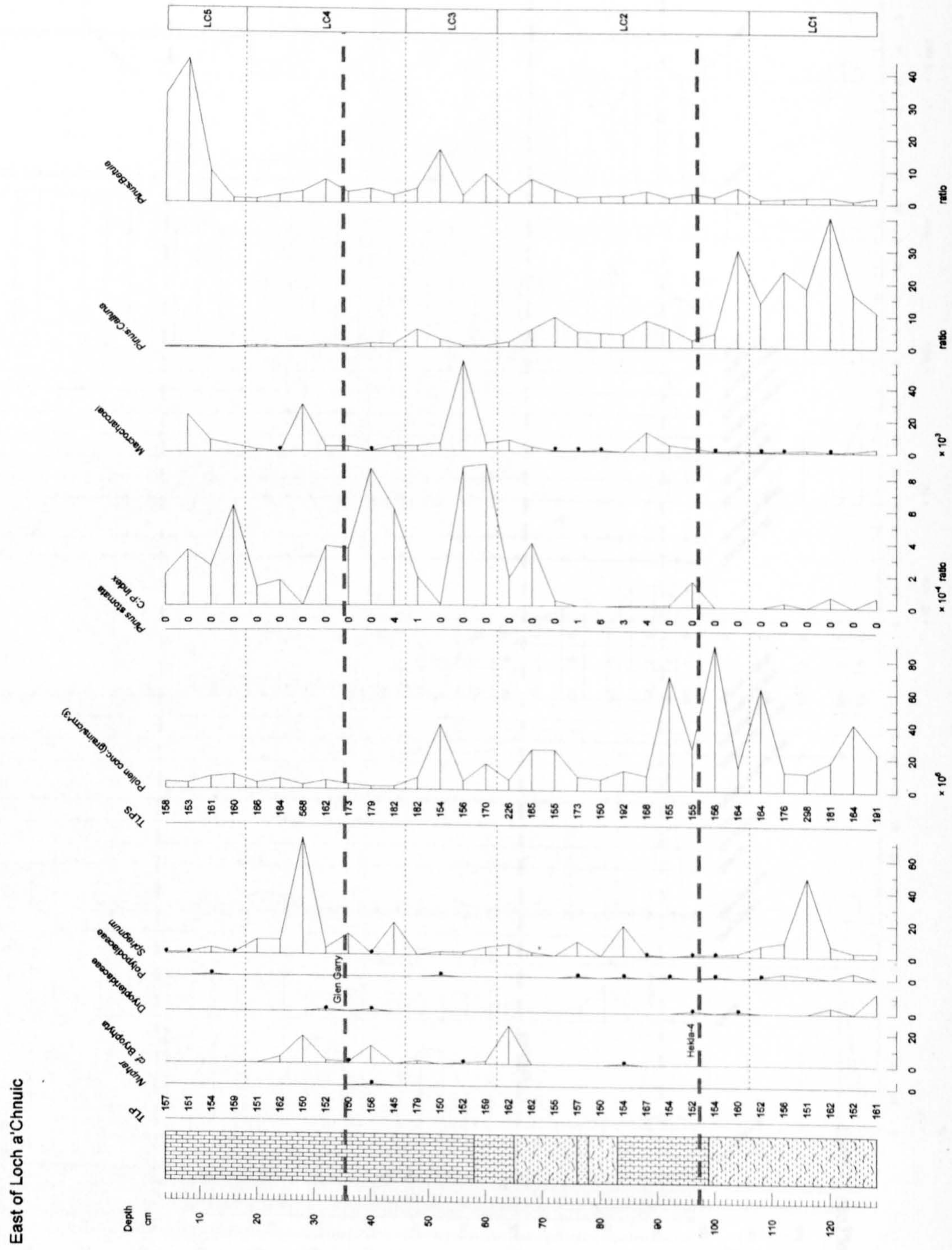


Loch an Spioraid

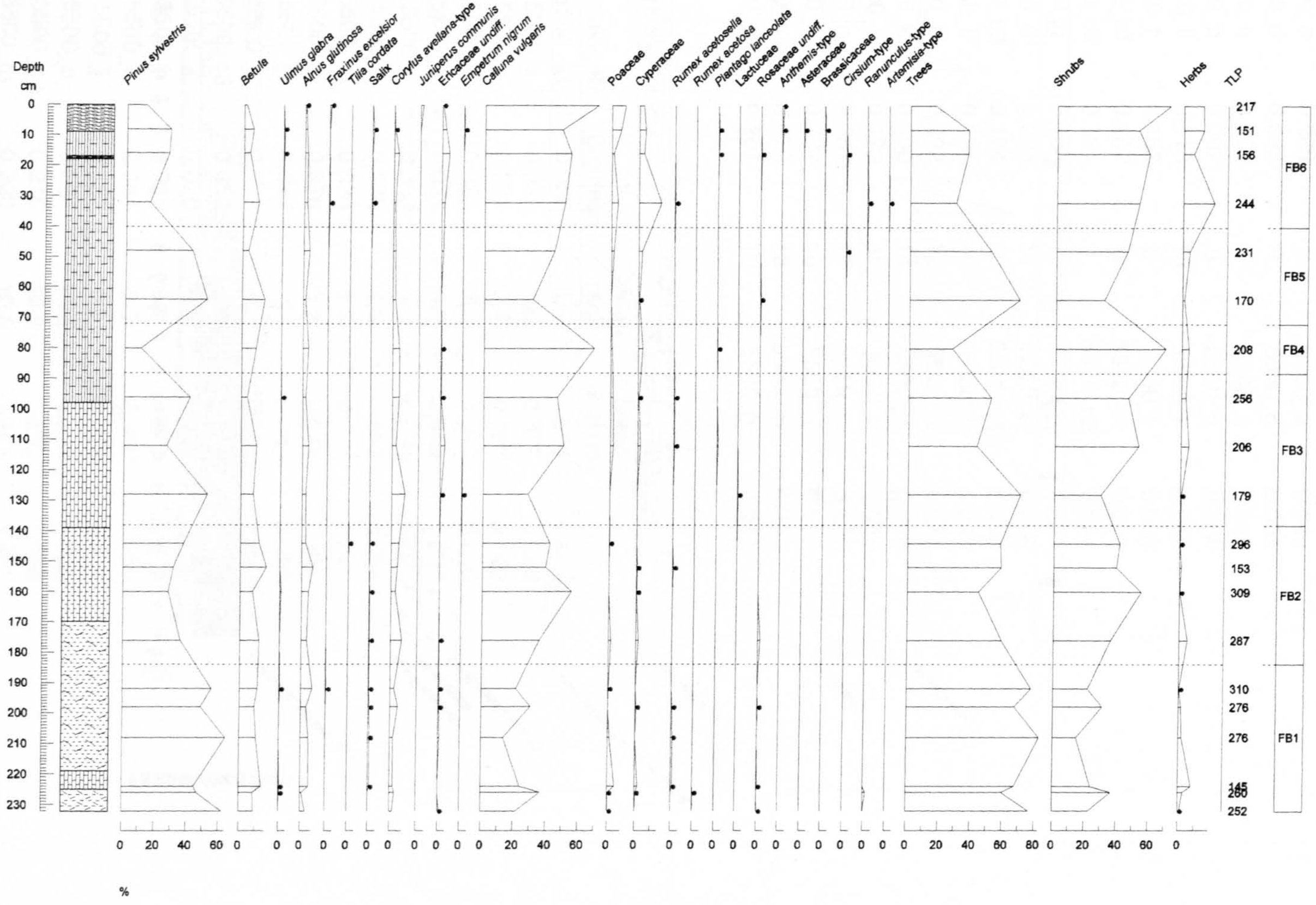


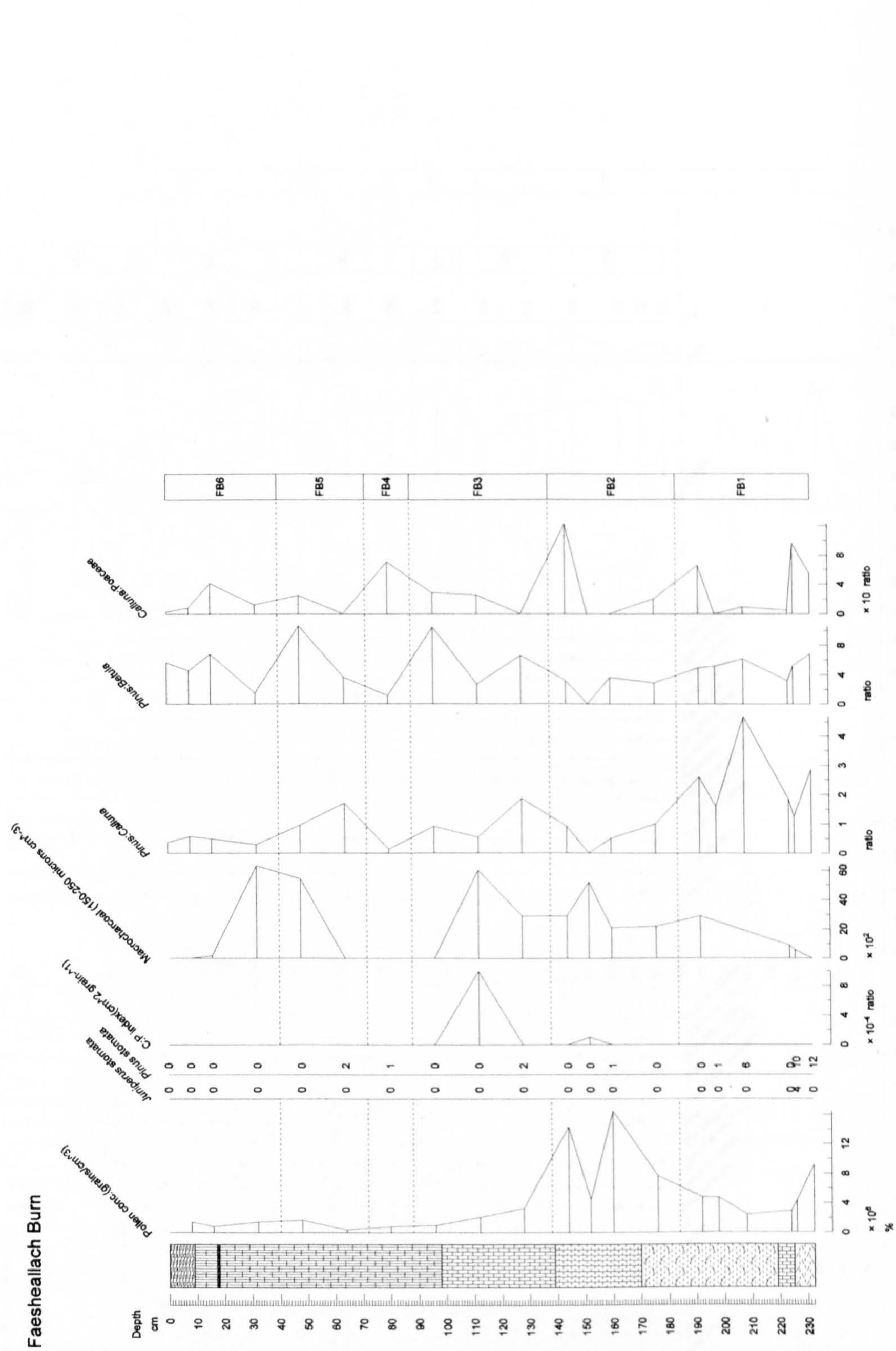
East of Loch a'Chnuic




East of Loch a'Chnuic
LC5
LC4
LC3
LC2
LC1
Depth
cm
TLP
Mupbar
d. Bryophyta
Dryopteridaceae
Polypodiaceae
Sphagnum
Glen Garry
Hekla-4
TLPS
Pollen conc.(grains/cm^3)
Pinus stomata
C.P Index
Meteochar.coal
Pinus.Calluna
Pinus.Betula
ratio
× 10^3
× 10^-4 ratio
× 10^6
%

Faesheallach Burn




Faesheallach Burn
Depth cm
0
10
20
30
40
50
60
70
80
90
100
110
120
130
140
150
160
170
180
190
200
210
220
230
Pollen conc.(grains/cm^3)
× 10^6
%
Juniperus stomata
Pinus stomata
C:P index(cm^2 grain^-1)
× 10^-4 ratio
Macrocharcoal (150-250 microns cm^-3)
× 10^2
Pinus:Calluna
ratio
Pinus:Betula
ratio
Calluna:Poaceae
× 10 ratio
FB6
FB5
FB4
FB3
FB2
FB1

Appendix 3.
Dissimilarity coefficients for 6400 cal. BP time slice.

Tore Hill			North Abernethy		
Rank	Analog ID	Distance	Rank	Analog ID	Distance
0	5500_a1	0.089	2	5500_a1	0.027
1	5500_a	0.089	5	5500_a	0.049
5	5500_d	0.093	7	5500_d	0.051
2	5500_c	0.090	4	5500_c	0.047
7	5500_b	0.097	8	5500_b	0.054
10	5500_l	0.118	10	5500_l	0.060
11	5500_f	0.133	6	5500_f	0.050
13	5500_c1	0.167	0	5500_c1	0.020
12	5500_c2	0.134	1	5500_c2	0.024
9	5500_g	0.104	13	5500_g	0.089
8	5500_e	0.098	11	5500_e	0.066
14	5500_c3	0.174	3	5500_c3	0.030
6	5500_i	0.094	15	5500_i	0.097
4	5500_h	0.092	12	5500_h	0.071
3	5500_k	0.090	14	5500_k	0.093
15	5500_j	0.178	9	5500_j	0.058
16	5500_n	0.261	17	5500_n	0.221
19	5500_o	0.337	16	5500_o	0.217
18	5500_m	0.270	18	5500_m	0.330
17	5500_p	0.267	19	5500_p	0.337

Carn a'Chnuic			Summary statistics		
Rank	Analog ID	Distance	Mean rank	Mean distance	s.d.
7	5500_a1	0.036	1.8	0.051	0.034
2	5500_a	0.032	1.6	0.057	0.029
0	5500_d	0.027	2.4	0.057	0.033
5	5500_c	0.035	2.2	0.057	0.029
1	5500_b	0.027	3.2	0.059	0.035
3	5500_l	0.033	4.6	0.070	0.044
6	5500_f	0.036	4.6	0.073	0.052
4	5500_c1	0.033	3.4	0.073	0.081
13	5500_c2	0.078	5.2	0.078	0.055
8	5500_g	0.047	6	0.080	0.029
12	5500_e	0.075	6.2	0.080	0.017
10	5500_c3	0.052	5.4	0.085	0.078
11	5500_i	0.070	6.4	0.087	0.015
15	5500_h	0.099	6.2	0.087	0.014
14	5500_k	0.081	6.2	0.088	0.006
9	5500_j	0.051	6.6	0.096	0.071
19	5500_n	0.227	10.4	0.237	0.022
16	5500_o	0.210	10.2	0.255	0.072
18	5500_m	0.223	10.8	0.274	0.053
17	5500_p	0.220	10.6	0.275	0.059

Dissimilarity coefficients for 4260 cal. BP time slice.

Forest Lodge			North Abernethy			Loch an Spioraid		
Rank	Analog ID	Distance	Rank	Analog ID	Distance	Rank	Analog ID	Distance
3.0	3830_b	0.056	20	3830_b	0.046	15	3830_b	0.092
1.0	3830_l	0.055	13	3830_l	0.036	24	3830_l	0.109
9.0	3830_k	0.071	16	3830_k	0.040	2	3830_k	0.078
2.0	3830_g	0.056	3	3830_g	0.028	23	3830_g	0.108
12.0	3830_u	0.079	18	3830_u	0.043	21	3830_u	0.102
0.0	3830_o	0.054	17	3830_o	0.043	11	3830_o	0.082
7.0	3830_q	0.060	15	3830_q	0.040	10	3830_q	0.082
14.0	3830_d	0.087	22	3830_d	0.058	12	3830_d	0.085
5.0	3830_r	0.059	10	3830_r	0.033	26	3830_r	0.122
13.0	3830_h	0.080	21	3830_h	0.051	18	3830_h	0.098
17.0	3830_s	0.093	8	3830_s	0.033	17	3830_s	0.097
16.0	3830_v	0.091	12	3830_v	0.036	20	3830_v	0.102
4.0	3830_bc	0.056	25	3830_bc	0.064	22	3830_bc	0.103
19.0	3830_t	0.113	19	3830_t	0.044	5	3830_t	0.079
6.0	3830_c	0.059	1	3830_c	0.027	7	3830_c	0.079
8.0	3830_n	0.066	7	3830_n	0.031	3	3830_n	0.078
10.0	3830_x	0.073	23	3830_x	0.060	14	3830_x	0.090
11.0	3830_z	0.073	24	3830_z	0.060	13	3830_z	0.090
15.0	3830_i	0.089	0	3830_i	0.026	9	3830_i	0.081
20.0	3830_j	0.114	14	3830_j	0.038	1	3830_j	0.078
22.0	3830_f	0.118	5	3830_f	0.029	25	3830_f	0.112
18.0	3830_a	0.094	2	3830_a	0.027	0	3830_a	0.078
21.0	3830_w	0.115	6	3830_w	0.031	6	3830_w	0.079
24.0	3830_p	0.151	11	3830_p	0.035	16	3830_p	0.094
23.0	3830_e	0.144	4	3830_e	0.028	8	3830_e	0.080
25.0	3830_m	0.179	9	3830_m	0.033	4	3830_m	0.079
27.0	3830_y	0.258	27	3830_y	0.112	19	3830_y	0.101
26.0	3830_aa	0.252	26	3830_aa	0.072	27	3830_aa	0.135

Dissimilarity coefficients for 4260 cal. BP time slice (cont.).

Faesheallach Burn			East of Loch a'Chnuic			Summary statistics		
Rank	Analog ID	Distance	Rank	Analog ID	Distance	Mean	sd	Mean rank
2.0	3830_b	0.062	12	3830_b	0.056	0.062	0.018	10.4
1.0	3830_l	0.061	7	3830_l	0.053	0.063	0.027	9.2
22.0	3830_k	0.093	0	3830_k	0.043	0.065	0.023	9.8
10.0	3830_g	0.074	19	3830_g	0.061	0.065	0.029	11.4
3.0	3830_u	0.062	2	3830_u	0.044	0.066	0.025	11.2
19.0	3830_o	0.091	20	3830_o	0.069	0.068	0.020	13.4
25.0	3830_q	0.099	17	3830_q	0.061	0.068	0.023	14.8
5.0	3830_d	0.067	4	3830_d	0.045	0.068	0.018	11.4
20.0	3830_r	0.091	1	3830_r	0.043	0.070	0.037	12.4
4.0	3830_h	0.066	13	3830_h	0.057	0.070	0.019	13.8
12.0	3830_s	0.080	6	3830_s	0.051	0.070	0.028	12.0
8.0	3830_v	0.070	8	3830_v	0.055	0.070	0.027	12.8
11.0	3830_bc	0.075	9	3830_bc	0.055	0.071	0.020	14.2
9.0	3830_t	0.074	3	3830_t	0.045	0.071	0.029	11.0
24.0	3830_c	0.099	26	3830_c	0.091	0.071	0.029	12.8
27.0	3830_n	0.102	22	3830_n	0.078	0.071	0.026	13.4
16.0	3830_x	0.088	10	3830_x	0.055	0.073	0.016	14.6
17.0	3830_z	0.088	11	3830_z	0.055	0.073	0.016	15.2
15.0	3830_i	0.085	25	3830_i	0.090	0.074	0.027	12.8
21.0	3830_j	0.093	18	3830_j	0.061	0.077	0.029	14.8
7.0	3830_f	0.068	15	3830_f	0.058	0.077	0.038	14.8
13.0	3830_a	0.081	27	3830_a	0.112	0.078	0.032	12.0
26.0	3830_w	0.101	21	3830_w	0.074	0.080	0.032	16.0
14.0	3830_p	0.084	5	3830_p	0.046	0.082	0.046	14.0
23.0	3830_e	0.097	23	3830_e	0.082	0.086	0.042	16.2
18.0	3830_m	0.088	16	3830_m	0.059	0.088	0.056	14.4
0.0	3830_y	0.055	14	3830_y	0.058	0.117	0.083	17.4
6.0	3830_aa	0.068	24	3830_aa	0.085	0.123	0.077	21.8

Dissimilarity coefficients for 2150 cal. BP time slice

Forest Lodge			East of Loch a'Chnuic		
Rank	Analog ID	Distance	Rank	Analog ID	Distance
0	2100BP_w	0.057	1	2100BP_w	0.061
3	2100BP_b6	0.062	7	2100BP_b6	0.096
9	2100BP_b15	0.064	2	2100BP_b15	0.062
1	2100BP_b11	0.058	12	2100BP_b11	0.100
7	2100BP_b10	0.064	9	2100BP_b10	0.098
4	2100BP_b13	0.062	14	2100BP_b13	0.103
2	2100BP_b12	0.059	19	2100BP_b12	0.116
22	2100BP_aa	0.070	0	2100BP_aa	0.059
5	2100BP_i	0.063	17	2100BP_i	0.115
8	2100BP_b9	0.064	16	2100BP_b9	0.108
19	2100BP_b8	0.068	6	2100BP_b8	0.084
16	2100BP_b16	0.067	10	2100BP_b16	0.099
10	2100BP_a	0.065	21	2100BP_a	0.118
21	2100BP_t	0.070	11	2100BP_t	0.100
29	2100BP_u	0.078	3	2100BP_u	0.065
11	2100BP_e	0.065	23	2100BP_e	0.121
27	2100BP_b3	0.073	8	2100BP_b3	0.097
32	2100BP_x	0.080	4	2100BP_x	0.074
6	2100BP_b1	0.063	31	2100BP_b1	0.138
34	2100BP_v	0.084	5	2100BP_v	0.075
18	2100BP_n	0.068	25	2100BP_n	0.124
13	2100BP_b5	0.065	33	2100BP_b5	0.143
33	2100BP_bb	0.084	13	2100BP_bb	0.102
28	2100BP_q	0.075	18	2100BP_q	0.116
25	2100BP_b14	0.072	22	2100BP_b14	0.120
15	2100BP_b2	0.066	32	2100BP_b2	0.143
12	2100BP_j	0.065	36	2100BP_j	0.148
30	2100BP_o	0.079	20	2100BP_o	0.118
35	2100BP_r	0.087	15	2100BP_r	0.107
24	2100BP_s	0.072	27	2100BP_s	0.126
14	2100BP_b7	0.066	38	2100BP_b7	0.150
17	2100BP_b	0.068	37	2100BP_b	0.149
26	2100BP_g	0.073	29	2100BP_g	0.137
20	2100BP_b4	0.069	42	2100BP_b4	0.162
23	2100BP_f	0.071	39	2100BP_f	0.155
37	2100BP_k	0.094	26	2100BP_k	0.126
42	2100BP_z	0.129	24	2100BP_z	0.122
39	2100BP_c	0.106	30	2100BP_c	0.138
43	2100BP_y	0.150	28	2100BP_y	0.129
31	2100BP_d	0.079	43	2100BP_d	0.174
41	2100BP_l	0.111	34	2100BP_l	0.146
40	2100BP_m	0.111	35	2100BP_m	0.146
36	2100BP_h	0.087	40	2100BP_h	0.158
38	2100BP_p	0.101	41	2100BP_p	0.160

Dissimilarity coefficients for 2150 cal. BP time slice (cont.).

Summary statistics		
Mean distance	s.d.	Mean rank
0.059	0.002	0.5
0.079	0.024	5
0.063	0.002	5.5
0.079	0.030	6.5
0.081	0.024	8
0.083	0.029	9
0.088	0.041	10.5
0.065	0.008	11
0.089	0.036	11
0.086	0.031	12
0.076	0.011	12.5
0.083	0.022	13
0.091	0.037	15.5
0.085	0.022	16
0.072	0.009	16
0.093	0.040	17
0.085	0.017	17.5
0.077	0.005	18
0.101	0.053	18.5
0.080	0.006	19.5
0.096	0.040	21.5
0.104	0.055	23
0.093	0.012	23
0.095	0.029	23
0.096	0.034	23.5
0.104	0.054	23.5
0.106	0.058	24
0.098	0.028	25
0.097	0.014	25
0.099	0.038	25.5
0.108	0.060	26
0.108	0.057	27
0.105	0.045	27.5
0.115	0.066	31
0.113	0.060	31
0.110	0.022	31.5
0.126	0.004	33
0.122	0.023	34.5
0.139	0.015	35.5
0.126	0.067	37
0.129	0.025	37.5
0.129	0.025	37.5
0.123	0.050	38
0.131	0.042	39.5